ESTUARIES AS HABITAT FOR A FRESHWATER SPECIES: ECOLOGY OF LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*) ALONG A SALINITY GRADIENT

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A Thesis

Submitted to

the Graduate Faculty of

Auburn University

in Partial Fulfillment of the

Requirements for the

Degree of

Masters of Science

Auburn, Alabama
May 10, 2007

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VITA

Alicia Jean Norris, daughter of Evlin Spitler and Mary Ellen Norris, was born on December 5, 1975 in Lebanon, Pennsylvania. In 1993, she graduated from Northern Lebanon High School in Fredericksburg, Pennsylvania. Her undergraduate degree in Marine Biology was completed in 1997 at the University of North Carolina at Wilmington located in Wilmington, North Carolina. Upon graduation, she completed an internship at Mote Marine Laboratory in Sarasota, Florida. From 1999-2001, she worked as a technical research assistant with the Massachusetts Cooperative Fish and Wildlife Research Unit at the University of Massachusetts in Amherst, Massachusetts. She began graduate school to pursue a master's degree at Auburn University in the Department of Fisheries and Allied Aquacultures in January of 2002. She currently works as a fisheries biologist with the Massachusetts Division of Fisheries and Wildlife in Westborough, Massachusetts.

THESIS ABSTRACT

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Master of Science, May 10, 2007
(B.S. University of North Carolina at Wilmington, 1997)

173 Typed Pages

Directed by Dennis R. DeVries and Russell A. Wright

Similar to the freshwater systems largemouth bass inhabit, the largemouth bass is a popular recreational sportfish in estuarine environments, like the Mobile-Tensaw Delta. However, catch rates of large (≥ 2.3 kg) largemouth bass are often low in these coastal systems, and coastal influences on this freshwater predator are not well understood.

In Chapter II, I investigated the potential effects of marine influence on largemouth bass along a downstream-upstream gradient in the Mobile-Tensaw Delta, Alabama. While salinity remained negligible upstream, the timing and absolute magnitude of peak salinity at our most downstream site varied among years. Mean length and catch rates did not vary predictably from downstream to upstream. A greater per gram diet biomass of vertebrates was generally consumed both downstream and upstream; however, invertebrates were consistently consumed throughout this system.

Condition (Wr) was generally high for all largemouth bass but was greater downstream than upstream in all years. Few largemouth bass age-4 and older were present, and survival was generally low across years throughout the study area. Growth to age-1 was greater downstream versus upstream in all years, with no differences occurring for older fish. Largemouth bass growth at all ages was greater for fish transplanted into freshwater from the Mobile-Tensaw Delta had a greater growth potential, but survival remained low in the absence of coastal influences.

In Chapter III, I combined three approaches to explore movement of adult largemouth bass in relation to salinity and angler displacement: external tagging, acoustic telemetry, and fish releases at tournaments. Movement patterns of downstream fish included remaining in protected channels near the release location, moving upstream as salinity increased (< 2‰), or moving into the main river channel. Fish upstream generally remained near the release site. Recaptures of largemouth bass tagged externally during regular sampling were typically found in the original tagging site (86−100% across years), while largemouth bass from a tournament tagging effort dispersed from the release point in < 23 days.

In summary, among-year abiotic variability was great, and salinity did not solely drive yearly patterns. Experimental and modeling approaches to better quantify the effects of interacting abiotic variables as well as those caused by angling on population characteristics of coastal largemouth bass.

ACKNOWLEDGEMENTS

I thank my advisors, Drs. Dennis DeVries and Russell Wright, for their excellent academic parenting skills. Their uncanny ability to recite lines from the movie "Airplane" diffused many long meetings. Thank you to Drs. Maurice Mettee and Gary Hepp for suggestions that improved this research and to Dr. Mettee for advice on acoustic telemetry. While the Mobile Delta, with its boat-sized alligators, people-eating wasps, life-sucking muck, and energy-draining heat, is a challenging work environment, it is also a uniquely beautiful and scientifically fascinating system. I sincerely thank Deborah Smith and Troy Farmer for their technical support. With Deborah's colorful humor, need to know everything, and heart-stopping fall into the alligator-infested abyss and Troy's constant state of exhaustion from doing more than humanly possible, field and lab work were rarely uneventful. I especially thank Tammy DeVries for her support and efficiency in the lab and keeping the snack box full and the lunch crew organized. Adam Peer, Ryan Baya, Stephen DeVries, Mike Lowe, David Glover, Andrew Rypel, and Michael Ross contributed valuable time to the project. Joe Zolczynski and Dave Armstrong from Alabama Division of Wildlife and Freshwater Fisheries provided us with logistical support and collaboration on research. For their encouragement, I extend appreciation to my family, especially my mother, Mary Ellen Norris; my brother, Christian; and my grandparents, Reginald and Jean Yorty. I also owe special thanks to Oscar Zelaya for being a part of my life at a difficult time and always pushing me to keep going.

Style Manual or journal used – Ecological Applications

Computer Software Used – Microsoft Word, Sigma Plot 8.0, Microsoft Excel, and SAS Version 8

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I. INTRODUCTION: IMPORTANT FACTORS FOR A FRESHWATER SPECIES IN AN ESTUARINE SYSTEM

Contribution of marine and freshwater input into estuaries and estuarine communities

Formed at the interface between marine and freshwater systems, estuaries are subject to temporal and spatial fluctuations in environmental characteristics, and are particularly influenced by salinity. Estuarine systems are strongly influenced, both by marine and freshwater inputs (Jassby et al. 1995). With the focus of previous studies seeming to be on linkages between estuarine and marine systems, few studies have incorporated the significance of flow or variability from riverine systems into and across estuarine systems (Schroeder 1978). This includes variability in salinity, channel and basin morphology, effects of tides and currents (Wheatly 1988), as well as the effects on water depth influenced by changes in flow (Bain et al. 1988) and tides (Kneib 1987). In comparison to estuarines that are primarily tidally-influenced, the flow regime in river-dominated estuaries may further influence fish communities by creating extensive low-salinity habitats, in which a higher proportion of freshwater to estuarine/ marine fishes may occur (Peterson and Meador 1994). Consequently, examining environmental variables associated with freshwater input into river-dominated estuaries may be important to understanding the community and trophic organization of these areas (Livingston et al. 1997)

Low salinity (limnetic and oligohaline) habitats may experience dramatic fluctuations in salinity more so than higher salinity waters, which may influence the stability of fish community composition (Rozas and Hackney 1984, Peterson and Ross 1991, Wagner 1999). Oligohaline (0.5−5‰) and tidal freshwater (< 0.5‰) habitats found in the upper reaches of estuaries tend to be occupied by a combination of estuarine, marine, and freshwater species, while the lower reaches of estuaries where salinities are higher (> 5‰) tend to contain primarily marine and estuarine species (Peterson and Ross 1991, Wagner 1999). As such, freshwater species appear to be more sensitive to the highly variable salinity of the freshwater/marine interface than marine species (Wagner 1999).

When considering estuaries along a salinity gradient (as in this study), species richness appears to be lower in oligohaline habitats, possibly due to greater changes in levels of abiotic factors (Rozas and Hackney 1984, Odum 1988, Wagner 1999). Reduced species richness in oligohaline habitats relative to higher salinity or strictly freshwater habitats is thought to benefit resident and transient inhabitants alike, by minimizing species interactions (i.e., reduced number of interspecific predators and competitors) (Rozas and Hackney 1984). However, some disagree by hypothesizing a spatially and temporally (seasonally) more diverse fauna created by this greater relative magnitude of change in environmental factors in low-salinity habitats (Peterson and Ross 1991, Peterson and Meador 1994). Therefore, the relationship between the variable abiotic conditions of low-salinity environments and the fish species using these habitats is still unclear.

Ecological significance of estuaries to fish communities

Previously, estuarine community ecology has concentrated on a detrital connection between salt marshes and upper trophic levels through several mechanisms (tidal subsidy, out-welling, and the detritus food chain) (Odum 1980). However, significant evidence suggests aquatic vegetation (Weinstein and Brooks 1983, Rozas and Odum 1988, Hettler 1989) and shallow water (Ruiz et al. 1993) habitats found in estuaries may also function as protection for marine and estuarine organisms seeking refuge from predators. Most estuarine research relevant to predator-prey interactions has been conducted in higher salinity marshes (Rozas and Hackney 1984). Evidence also suggests similarities in the protective value of shallow, vegetated marsh habitats between tidal freshwater/oligohaline estuarine zones and comparable habitats in higher salinity zones (Rozas and Odum 1988). Though fish of freshwater origin are present in these upper estuarine zones, most studies have focused on the use of these shallow, vegetated habitats by fishes of marine or estuarine origin. Hence, the exact role freshwater fish play in these habitats and the overall communities inhabiting these environments remains unknown (Peterson and Meador 1994).

The conventional idea of reduced predation risk implies that fewer large predators occupy these shallow, vegetated environments than deeper, more open waters in estuaries (Rozas and Hackney 1984, Rozas and Odum 1988). Sheaves (2001) reviewed this hypothesis and determined fundamental inconsistencies across studies, suggesting predation may play a more significant role in the survival of juvenile estuarine fish than previously thought. Given the presence of fish that become piscivorous as juveniles, shallow, vegetated habitats may not provide as much refuge as once thought. Also, marine and estuarine piscivores tend to be absent from low salinity habitats, while large, freshwater piscivores, i.e. largemouth bass (*Micropterus salmoides*) and longnose gar (*Lepisosteus osseus*), are considered to be present in low numbers by some (Rozas and Hackney 1984). However, large, freshwater piscivores inhabiting estuaries are poorly studied, which could add to a lack of understanding as to their abundance and role as predators in these environments.

Coastal Largemouth Bass Populations

The broader concepts of estuarine community ecology discussed above provide a useful framework within which to base our knowledge of a more specific interest to this study, coastal largemouth bass populations. Such populations are found in coastal U.S. waters from the mid-Atlantic to the Gulf of Mexico. As with largemouth bass populations in purely freshwater systems, coastal largemouth bass populations support a popular recreational fishery. However, limited studies throughout the range of coastal bass have been conducted (D. L. Armstrong, ADCNR, unpublished report), and several areas of coastal largemouth bass research remain unclear (e.g., salinity tolerance, growth and condition, diet composition, movement, and predation risk). These areas are briefly summarized in the following sections.

Salinity tolerance. Although largemouth bass have been found in salinity as high as 17.5‰ (Swingle and Bland 1974), adult and juvenile largemouth bass from both coastal and freshwater populations preferred less than 3‰ salinity (Meador and Kelso 1989). Adult largemouth bass held at varying salinities have shown a limited tolerance for salinities over 8‰ with mortality occurring within 120 days of salinity held constant at 12‰ (Meador and Kelso 1990b). Juvenile largemouth bass, which appear to tolerate salinities up to 10‰ and do better than adults in salinities approaching 12‰, may have a higher tolerance for salinity than adult largemouth bass (Susanto and Peterson 1996). Largemouth bass are thought to osmoregulate more efficiently at salinities lower than 4‰ due to reduced energetic costs, which may contribute to preferences for lower salinity habitats (Meador and Kelso 1990a).

Growth and condition. Adult largemouth bass in coastal populations typically exhibit reduced growth rates and reach smaller sizes relative to largemouth bass from freshwater systems. Predator crowding, similar to what would be expected at high densities in freshwater ponds, was an early explanation for this growth pattern (Swingle and Bland 1974). In the case of coastal environments, movement of largemouth bass away from salinity into upstream areas was thought to create crowded conditions for largemouth bass (Swingle and Bland 1974). More recent studies have begun to favor other explanations for reduced growth as discussed below. While growth differences resulted in higher condition factors for coastal largemouth bass, Hallerman et al. (1986) found no significant genetic differences between populations as expected and suggested an environmental effect on growth. Meador and Kelso (1990b) suggested this lack of genetic difference and high condition factor to be evidence of an alternative growth pattern caused by environmental factors, which included diet composition, prey availability, predation risk, and habitat complexity.

Diet composition. A few studies have shown that largemouth bass have a high proportion of invertebrates in their diets (Colle et al. 1976, Lorio et al. 1982, Meador and Kelso 1990b). However, fish are considered the prey type for which maximum growth in largemouth bass occurs (Crowder and Cooper 1979, Hoyle and Keast 1987, Savino and

Stein 1989). Growth rates of largemouth bass consuming a diet of invertebrates may be affected (Guier et al. 1978, Meador and Kelso 1990b). Additionally, invertebrate prey (i.e., shrimp and crab) found in diets of coastal largemouth bass are potentially marine-derived (Peterson 1991). Consumption of marine-derived prey may influence growth of a freshwater fish, like largemouth bass, but this relationship has not been studied.

Movement. As salinity increases, adult bass reportedly move from higher salinity waters to presumably lower salinity waters, while smaller adult largemouth bass remain in higher salinity waters (Swingle and Bland 1974, Meador and Kelso 1989). Because evidence suggests a preference by both juvenile and adult bass for low salinity or fresh water, one would expect movement out of these areas by smaller adults as well. Meador and Kelso (1989) suggested that salinity may be the impetus for movement of largemouth bass, while predation risk may confine the smaller, more vulnerable adults from movement to preferred habitats as salinity levels rise.

Predation risk. Largemouth bass are typically considered a top piscivore in most freshwater systems (Howick and O'Brien 1983, Meador and Kelso 1990b) and are a keystone predator capable of initiating top-down effects (Carpenter et al. 1985, 1987; Mittelbach et al. 1995). Unlike adult largemouth bass in many freshwater systems throughout the United States, coastal adult largemouth bass populations appear to be occupying the role of an intermediate predator and risk of predation was suggested as a possible cause for a lack of movement into more profitable habitats (Meador and Kelso 1990b). An indication of this is consumption of invertebrate prey consumed by adult largemouth bass in coastal communities (Colle et al. 1976, Lorio et al. 1982, Meador and Kelso1990b). Trade-offs in foraging rate due to predation risk have been documented in freshwater systems (Werner and Hall 1988). Large piscivores also frequent areas similar to coastal largemouth bass (Meador and Kelso 1990b). The Mobile-Tensaw Delta is also home to piscivores capable of consuming adult largemouth bass such as, gar (*Lepisosteus spp.)*, bowfin (*Amia calva)*, southern flounder (*Paralichthys lethostigma)*, and chain pickerel (*Esox niger)* (unpublished data). Similar to Meador and Kelso (1990b), wounded and scarred largemouth bass are common (nearly 1 out of 5 captured adult largemouth bass in one sampling trip) in our study area (personal observation).

In summary, a spatially and temporally dynamic abiotic environment, such as the Mobile-Tensaw Delta, can influence various population characteristics of coastal largemouth bass. Likewise, this freshwater predator may influence juvenile marine and estuarine species using estuaries as nursery habitat. However, it is uncertain to what extent freshwater residents in estuaries both directly benefit from or influence other species in these environments. Understanding the interactions between the freshwater and marine ecosystems will be imperative to identifying the role of largemouth bass in coastal systems.

II. FRESHWATER-MARINE LINKAGES: THE ROLE OF A FRESHWATER SPECIES *(MICROPTERUS SALMOIDES)*

INTRODUCTION

Although ecosystems are often defined by relatively distinct boundaries, these boundaries may be temporally and spatially dynamic, promoting interactions between systems otherwise thought to be self-contained. Trans-boundary subsidies of energy, nutrients, and organisms have been widely documented for many ecosystems and habitats and can be facilitated by abiotic processes as well as movement of organisms (Polis et al. 1997). Such subsidies often occur when contributions from a resource-rich, donor ecosystem enhance productivity to a resource-poor, recipient ecosystem (Polis et al. 1997). Nutrients and detrital matter from cross-boundary contributions can control lower trophic levels in recipient ecosystems (Odum 1980, Vanni et al. 2004) and sometimes indirectly influence higher trophic levels (Polis and Hurd 1996, Pace et al. 2004, Carpenter et al. 2005, Vanni et al. 2005). Also, upper trophic levels are sometimes directly influenced (e.g., population density) by prey subsidies to consumers (Rose and Polis 1998, Henschel 2004, Willson et al. 2004, Barrett et al. 2005, Baxter et al. 2005). In addition, the flow of energy, nutrients and organisms, and hence productivity, has been perceived as unidirectional, typically from terrestrial to aquatic ecosystems; however, reciprocal fluxes (Vander Zanden and Sanzone 2004, Baxter et al. 2005, Willson et al. 2004) among multiple ecosystems may be more likely.

Estuaries represent boundaries between freshwater and marine ecosystems and are highly productive habitats as evidenced by nutrients carried by river input as well as runoff directly from bordering terrestrial systems (Livingston et al. 1997, Polis et al. 2004). Therefore, estuaries may be influenced by multi-directional fluxes among ecosystems (e.g., terrestrial, freshwater, and marine). Subsidies directly from marine to terrestrial ecosystems have been found (Polis and Hurd 1996, Rose and Polis 1998, Barrett et al. 2005). The potential for reciprocal subsidies between marine and freshwater ecosystems via the estuarine ecotone should also exist but have not been defined as such in the subsidy literature to the extent other linked ecosystems have.

Estuaries are typically sub-divided based on standardized salinity boundaries (e.g., tidal freshwater, < 0.5‰; oligohaline, < 5.0‰; mesohaline, < 18.0‰; polyhaline, < 30.0‰; Cowardin et al. 1979) along a freshwater-marine continuum. Depending on the amount of freshwater input, potentially extensive areas of environmental overlap between marine and freshwater ecosystems can occur, especially in the tidal freshwater and oligohaline portions of the estuary. The position of the salt wedge within the estuary, absolute salinity levels, and the rate of salinity fluctuation is largely controlled by the quantity and seasonality of freshwater discharge (Peterson and Ross 1991, Jassby et al. 1995). Variability in freshwater input can also directly influence the continual advance and retreat of the salt wedge upstream (Peterson 2003).

The strength of cross-boundary trophic interactions may also be considerable between marine and freshwater ecosystems where freshwater input is substantial and creates extensive areas of environmental overlap. For instance, input of nutrients and lower trophic level organisms (e.g., phytoplankton and algae) from freshwater flow can be responsible for the strength of bottom-up forces and productivity in estuaries (Livingston et al. 1997). Also, subsidies and increased estuarine productivity from the marine ecosystem can result from tidal action (Odum 1980). Although marine, estuarine, and freshwater species can be found throughout estuaries, physiological tolerances to salinity vary and limit species distributions (Wheatley 1988, Dunson and Travis 1991). Generally, the distribution and abundance of freshwater species are more limited by increasing salinity than marine species, while marine and estuarine species are less limited by decreasing salinity than freshwater species (Peterson and Ross 1991). The spatially and temporally heterogeneous environment in estuarine systems allows for a highly diverse species assemblage of invertebrates and fish inhabiting oligohaline and tidal freshwater habitats and subsequently increases mixing among marine/estuarine and freshwater species (Peterson and Ross 1991).

Research has shown that upstream, low-salinity areas also are valued as nursery habitat and refuge from predation for juveniles of marine and estuarine species (Boesch and Turner 1984, Rogers et al. 1984) by providing similarly shallow, vegetated, and often turbid habitat as downstream portions of estuaries (Weinstein and Brooks 1983, Kneib 1987, Rozas and Odum 1988, Hettler 1989, Baltz et al. 1993, Ruiz et al. 1993). Although larger marine and estuarine predators may be less abundant in estuaries, predation may influence survival of juvenile estuarine fish more than once thought (Sheaves 2001). For example, marine and estuarine piscivores are present in shallow, vegetated habitats and can become piscivorous as juveniles. Another aspect to consider is the presence of large freshwater predators in estuaries (Rozas and Hackney 1984). However, the effect of larger freshwater predators (e.g., bowfin *Amia calva*, largemouth bass *Micropterus* *salmoides*, and gar *Lepisosteidae* spp.) inhabiting the lower salinity portions of these nursery areas on the estuarine community is rarely considered and remains poorly understood.

Largemouth bass is one freshwater predator common in low-salinity environments of U.S. Gulf and Atlantic coast estuaries (Meador and Kelso 1990b). As in freshwater systems, largemouth bass inhabiting coastal systems are a popular recreational sportfish (Nack et al. 1993, Richardson-Heft et al. 2000, Krause 2002, Markham et al. 2002), even though reduced growth and low catch rates of large (≥ 2.3 kg) coastal largemouth bass have been found in comparison to largemouth bass from strictly freshwater populations (Tucker 1985, Meador and Kelso 1990b, Nichols and McHugh 2002, Haffner et al. 2003).

While largemouth bass are likely not to remain in high-salinity water due to physiological constraints, the distribution of largemouth bass in relation to salinity and subsequently the extent of their downstream position in estuaries are uncertain. Although largemouth bass have been collected in relatively high salinities (17.5‰; Swingle and Bland 1974), experimental work suggests that at times of increasing salinity, both coastal and freshwater largemouth bass seek salinities ≤ 3‰ (Meador and Kelso 1989). Thus far *in situ* research is limited, but one Louisiana study suggested movement away from the study area, potentially to upstream, freshwater areas, once salinity reached 5‰ (Meador and Kelso 1989). Additionally, largemouth bass can experience mortality when held at salinities ≥ 12‰ for prolonged periods (120 days) (Meador and Kelso 1990a). Because of variability in freshwater flow, the shifting marine-freshwater boundary, and the ability of marine and estuarine species to move across the marine-freshwater boundary, largemouth bass are potentially exposed to marine influences in the form of both salinity and marine- and estuarine-derived prey and predators.

It is uncertain to what extent a freshwater predator, like largemouth bass, may benefit from potential marine/estuarine subsidies. Largemouth bass inhabiting coastal environments that are part of larger river systems are likely to experience both freshwater and marine influences. This interplay between the freshwater and marine ecosystems clearly will be important to the success of largemouth bass in coastal systems.

METHODS

Study Area

The rivers of the Mobile Basin Watershed drain portions of four states (Alabama, Mississippi, Tennesse, and Georgia) and empty into the Alabama and Tombigbee Rivers, which converge to form the Mobile River (Fig. 1). As the Mobile River flows downstream toward the Mobile Bay, it forms an 8,224 ha riverine complex encompassing an intricate network of rivers, creeks, bays, lakes, wetlands, and bayous, known as the Mobile-Tensaw Delta (Armstrong et al. 2000). The Mobile-Tensaw Delta is the fourth largest river delta in the United States (Tucker 1985) and spans a length of nearly 55 km and a width as great as 15 km (Fig. 1). Terrestrial habitat ranges from hardwood forests upstream to brackish marshes downstream. The Mobile-Tensaw Delta remains largely undeveloped upstream, and downstream the city of Mobile lies along the western shore and a series of smaller, but rapidly developing communities can be found along the eastern shore.

This river-dominated system has an average discharge rate of 1,750 m^3/s (Schroeder 1978). At highest average annual discharge rates (7,000 m^3/s), salinities < 2‰ can be maintained as far south as the middle of the Mobile Bay, while salinities of 4−10 ‰ can be observed in the upper part of the Mobile Bay during periods of low discharge (< 500 m^3/s; Schroeder 1978). During flood conditions, discharge rates as high as 11,500 m^3/s have been recorded and can create near limnetic conditions throughout most of the Mobile Bay (Schroeder 1978).

Seasonal variation in wind direction can also affect the position of the salt wedge in this system. For example, northerly winds are typical of colder months and may increase riverine influence, while southerly winds occur most often in warmer months and may increase marine influence (Schroeder 1978). Except at maximum amplitude, tidal influence (average tidal range < 0.5 m) on salt water intrusion is thought to be minimal (Schroeder 1978).

Site Description

Our study area is located within the lower portion of the Mobile-Tensaw Delta. Six fixed sites were primarily sampled along a downstream-upstream gradient. From downstream-upstream, these sites are D'Olive Bay, Bay Minette Bay, Crab Creek, Gravine Island, McReynold's Lake, and Dennis Lake (Fig. 1). Sites were selected to incorporate available habitat types along a downstream-upstream salinity gradient. Habitat types include large main river channels, smaller river and creek channels, and large embayments and bayous. These habitat types can be found throughout the Mobile-Tensaw Delta, but riverine habitats are generally best represented upstream and open habitats are more common downstream.

Both Dennis Lake (5 m total depth) and McReynold's Lake (4 m total depth) are upstream sites. Habitat at these sites is characterized as small, river channels with thickly forested shorelines. McReynold's Lake is a heavily vegetated, wind and flow protected site, whereas Dennis Lake has less abundant aquatic vegetation and is less protected from wind and flow. Gravine Island and Crab Creek are both mid-stream sites. Habitat transitions from forested riparian zones to marsh-lined riparian zones and dense aquatic vegetation is found at both sites. Gravine Island (~ 8 m total depth) is an unprotected main channel site with a wide, shallow littoral zone, while Crab Creek (~ 3 m total depth) is a smaller, protected distributary. Downstream sites are Bay Minette Bay and D'Olive Bay (both ~ 2 m total depth), both with marsh-lined riparian zones, abundant aquatic vegetation, and a lack wind protection. Bay Minette Bay is more protected from flow than D'Olive Bay, and flow in D'Olive Bay has been altered due to the construction of the Causeway (90/98).

Another downstream sample site was the Below Causeway site (~ 4 m total depth), which was substituted for D'Olive Bay primarily during 2002 sampling when access to D'Olive Bay was prohibited due to shallow water. Fish were not collected here during 2003 or 2004. This site is an unprotected, marsh-lined, main channel and has been historically affected by road development (e.g., Interstate-10, Route 90/98). Largemouth bass were also collected from Monroe County Lake, Monroe County, Alabama. This impoundment is a state-managed, public fishing, freshwater lake that was renovated and re-stocked with largemouth bass from the Mobile-Tensaw Delta in 1999.

Field Collection

Fish were sampled using pulsed-DC electrofishing (Smith-Root, Inc.; DC Electrofisher, 7.5 GPP, 7,500 W). Two 15-minute boom electrofishing transects were completed in nearshore waters < 2 m deep and were primarily used to collect adult largemouth bass and other larger fish (> 150 mm). Prod-pole electrofishing (Smith-Root, Inc.) consisted of three, 10-min transects in shallower, shoreline areas and was intended to replace seining, which was not possible due to habitat complexity (e.g., cypress knees, submerged roots, etc.) and a lack of firm substrate. This gear type was primarily used to sample juvenile fish and smaller-sized fish species (≤ 150 mm).

Water chemistry data were collected monthly at a deep-water location within each site. Depth profiles of salinity (‰), temperature (°C), conductivity (µS or mS), and dissolved oxygen ($mg \cdot L^{-1}$) were collected at these locations. In addition, secchi depth was measured, and a water sample collected for determination of turbidity (NTU) and chlorophyll-a concentrations in the laboratory. Temperature was obtained from HOBO temperature data loggers (Onset, Inc.) placed at each site (1−2 m depth) and set to record temperature every 2 hours.

All adult largemouth bass (age-1+; typically > 150 mm) were measured (nearest mm TL) and weighed (nearest g). As faster-growing juveniles and slower growing adults could overlap in size, a sub-sample of fish within this questionable size range (100−200 mm) were returned to the lab to verify age of fish collected. Diets of up to 30 adult largemouth bass were collected monthly at each site using acrylic tubes (Van Den Avyle and Roussel 1980). When necessary, prey items were extracted with forceps. Diets were placed in labeled bags, held on ice, and returned to the laboratory for processing. Most adult largemouth bass were released in the field after processing; however, each fall a sample of up to 20 adult largemouth bass were kept from each site for age and growth determination. For comparison of age and growth with largemouth bass from the Mobile-Tensaw Delta, a minimum of 30 adults were also sampled in fall 2004 from Monroe County Lake.

Laboratory Processing

<u>Largemouth bass.</u> Largemouth bass diet samples were sieved (500-µm mesh size) to remove excess water and placed under a dissecting microscope. Prey items were identified to species for fish and to order or family for insects, gastropods, amphibians,

and reptiles. Partially digested prey items were identified to the lowest possible taxonomic level. Prey items were measured (nearest mm) using a ruler for larger prey items and an ocular micrometer for smaller prey items. Measurements of up to 10 randomly selected individuals of each prey type were made from each largemouth bass diet, and remaining individuals were counted. Fish prey measurements generally included total length, standard length, backbone length, or otolith length. Carapace widths, claw lengths, or paddle lengths (blue crabs only) were taken for crabs. Telson, uropod, carapace, or claw (crayfish only) lengths were taken for shrimp and crayfish. Head width, body length, or wing length was measured for insect prey items. Shell widths were measured for gastropods, and snout-vent lengths were measured for amphibians and reptiles.

Fall-collected largemouth bass (for age and growth) were measured (nearest mm TL) and weighed (nearest g). Stomachs of each bass were removed, placed in labeled jars containing ethanol, and processed as described above. Both sagittal otoliths were extracted and placed in labeled vials. To aid in viewing annular rings, whole otoliths were placed in a glycerine solution (DeVries and Frie 1996) and examined using a dissecting microscope. Individual annuli were counted, and each otolith was independently aged by two readers. For those otoliths on which readers disagreed, a third reader was used. If all three readers disagreed or if otoliths could not be read, they were sectioned (Maceina 1988) and read using the same double-blind approach described above for whole mounted otoliths. Using an ocular micrometer, the length to each annulus and otolith radius was measured from the otolith nucleus.

Data Analysis

Environmental variables. Monthly salinity patterns were compared across years to determine potential differences in the magnitude and timing of peak salinity among sites along a downstream-upstream gradient. The upstream extent of the salt wedge was obtained by plotting monthly surface and bottom salinities for sites experiencing salinity. Daily mean temperatures were calculated to compare trends among sites.

As there are currently no USGS stream gages present along the eastern length of the Mobile-Tensaw Delta, water-level data was obtained from long-term data collected by the USGS at stream gage #002470629 located at the Barry Steam Plant on the Mobile River at river mile 31.0 near Bucks, Alabama. Mean daily river stage (m above sealevel) was compared among years (2002-2004) and was used to describe water-level fluctuations within the Mobile-Tensaw Delta.

An estimated 95% of water flowing through the Mobile-Tensaw Delta is accounted for by input from the Alabama and Tombigbee rivers (Schroeder 1978). Stream-flow for the Mobile-Tensaw Delta was estimated by summing stream-flow from USGS stream gage #02428400 on the Alabama River at Claiborne Lock and Dam near Monroeville, Alabama and USGS stream gage #02469761 on the Tombigbee River at Coffeeville Lock and Dam near Coffeeville, Alabama for 2002-2004 (Braun and Neugarten 2005). Provisional data were used after 30 September 2003, and data were missing between 30 September and 3 November 2003.

Largemouth bass. In order to maintain a standardized approach and reduce the potential for gear bias in our results, most data analysis consisted of largemouth bass collected by boom electrofishing only. However, low numbers of bass were common and largemouth bass collected from both gear types were included in the age and growth and diet composition analyses. Sites considered to be downstream from our sampling were D'Olive Bay, Below Causeway (2002 only), Bay Minette Bay, and Crab Creek. Sites considered to be upstream were Gravine Island, McReynold's Lake, and Dennis Lake. Significance levels for all statistical tests were $\alpha < 0.05$.

Mean size, catch rates, and relative weight. Proportions of larger fish were obtained by calculating values of indices, as described in Anderson and Neumann (1996), for Proportional Stock Density (PSD; ≥ 300 mm), Relative Stock Density-Preferred (RSD-P; ≥ 380 mm), Relative Stock Density-Memorable (RSD-M; ≥ 510 mm), and Relative Stock Density-Trophy (RSD-T; ≥ 630 mm).

Analysis of variance (ANOVA) tests were used to determine differences in mean monthly length (mean TL in mm) and catch rate (mean CPE in $\#\cdot hr^{-1}$). A two-way ANOVA (site and month) with an interaction effect was used to test for differences in mean TL among sites. Repeated-measures split-plot ANOVAs were designed to identify among-site and among-year differences in mean CPE. For each year, the among-site main plot consisted of site as the replicate, transect as the treatment variable, and a site*transect interaction term, which accounted for the main-plot experimental error. The sub-plot was defined with the month effect and a site*month interaction term, which together accounted for the remaining error. By individual site, the among-year main plot consisted of year as the replicate, transect as the treatment variable, and year*transect as the interaction term accounting for the main-plot experimental error. The sub-plot was defined with a month effect and month*year interaction term, which together account for any remaining error. All within-year variation for mean TL and mean CPE was determined through one-way ANOVA tests, using site as the dependent variable and month as the treatment variable. For all multiple comparisons, Duncan's Multiple Range Tests ($P < 0.05$) were conducted, where significant site, year, or month differences ($P < 0.05$) were found in ANOVA tests.

Mean CPE for all largemouth bass and mean relative weight (Wr) by size groups of largemouth bass were further analyzed by an average rank analysis, in which means for CPE or Wr were ranked from 1 (lowest) through 6 (highest) for each month within years (2002−2004). Mean Wr analysis included only fish > 150 mm (Wege and Anderson 1978, Anderson and Neumann 1996). Fish were categorized by size for ranking of mean Wr (small = 150-250 mm, large > 250 mm). Means with equal values were both assigned the same rank, which was the average of the whole numbers that would have been assigned to either number had there been no tie. Ranks were then averaged by site and standard errors determined. Site differences were determined using a one-way ANOVA, and comparisons were made using Duncan's Multiple Range Tests ($P < 0.05$).

A two-dimensional plot of catch rates by salinity and catch rate by temperature was tested with a 2-dimensional Kolmogorov-Smirnov (2DKS) test, as described in Garvey et al. (1998). A 2DKS analysis is used when correlation and regression analyses are deemed inappropriate and can be used to determine whether a non-random pattern exists with binary data combinations. This test determines potential threshold values of the independent variables where the probability of higher CPE changes. The threshold value, D, was used to indicate the level of salinity or temperature, where probabilities of higher catches change.

Age and Growth. For age and growth analyses, largemouth bass from our field collections and those from the Alabama Division of Wildlife and Freshwater Fisheries (ALDWFF) were combined. Although similar sampling techniques were used, the sites sampled by the ALDWFF varied among years, while our sites remained fixed in all years. Hence, sites were grouped into more general categories of downstream and upstream regions, using the downstream end of Gravine Island as an arbitrary boundary between regions.

The distribution of largemouth bass across age groups was determined by age-frequency distributions. Proportions of largemouth bass present by age class were separated by downstream and upstream regions. An age-frequency distribution was also created for Monroe County Lake fish.

Catch-curve regression analysis (age vs. ln #/age class) was used to determine an annual rate of survival obtained from the slope of each catch curve regression. Because of low numbers of older individuals, only fish ages 1−5 from downstream and upstream regions were included. Survival rates for fish from Monroe County Lake did not include fish older than age-3, because those were the only year classes produced in this lake.

From annular measurements, back-calculated length-at-age for individual fish could be determined using the direct proportion method (DeVries and Frie 1996). Back-calculated total lengths were then averaged for all individuals by age class.

Yearly growth curves were plotted based on age class vs. mean back-calculated total length. Differences in length-at-age between downstream and upstream regions of the Mobile-Tensaw Delta were analyzed using paired t-tests. Similarly, differences in growth-at-age between fish from Monroe County Lake and fish from the Mobile-Tensaw

Delta (upstream region only) were analyzed using paired t-tests. All p-values were Bonferroni corrected.

Diet Composition. Fish were grouped by upstream and downstream region and by season defined as winter (December–February), spring (March−May), summer (June−August), and fall (September−November). Diet composition was determined by converting lengths obtained for individual diet items into biomass. In order to assign a prey identification to all unidentified diet items, identified prey were classified into various site*time combinations (e.g., site by month, season, or year; region by month, season, or year). The narrowest site* time combination yielding $N \geq 10$ identified prey items was used. The proportion of identified prey items for these site*time combinations was determined and a prey identification was assigned by using a random number generator for numbers between 0 and 1. Once unidentified prey received identification codes, prey without sizes were assigned a mean size from identified prey items using similar site* time combinations discussed above and were combined with identified prey to obtain estimates of diet biomass.

For conversion to biomass estimates, length:wet weight regressions were taken from the literature where possible (Schoener 1980, Smock 1980, Pace and Orcutt 1981, Sage 1982, Kushlan 1986, Benke et al. 1999). If regressions were unavailable in the literature, length:wet weight regressions were developed from length and weight data obtained for species from our field collections. Slope and intercept values taken from the literature and created with our data for regression equations are available in Appendix 8.

Mean per gram diet biomass was then determined by dividing the total prey biomass consumed of an individual by the wet weight of the individual largemouth bass.

Individuals consuming high and low prey biomass were adjusted, and mean per gram diet biomass (p; g prey biomass$\cdot$g^{-1} individual wet weight) was arcsin transformed using the following equation:

$$t(p) = (360/(2pi))*(arcsin(SQRT(p)))$$

where t(p) is the angle resulting from the arcsin transformation of p, Π is the mathematical constant pi = 3.14159, and 360 is the number of degrees in a circle. Tests of significance used arcsin transformed values of the mean per gram diet biomass. Mean arcsin transformed per gram diet biomas values were obtained based on categories, such as invertebrates and vertebrates or prey origin (freshwater, estuarine, and marine), and a two-way ANOVA with an interaction effect identified differences between regions and within years. For ease of interpretation, untransformed means [g prey$\cdot$g bass^{-1}] or percentages of untransformed means were reported in results and figures.

RESULTS

Environmental Parameters

Timing and magnitude of the occurrence of salinity (1 meter depth) varied among years and sites (Fig. 2). Increasing salinity at downstream sites occurred earliest in 2002 (May−August), latest in fall 2003 (September−November), and intermediate in 2004 (August−November). Peak salinity at D'Olive Bay, our most downstream site, ranged from 4.8−9.3‰ across years. During peak salinity, the salt wedge was detectable at Gravine Island, a deeper (≥ 8 m), main channel site, where peak bottom salinity ranged from 13.5−15.6‰, and surface salinity ranged from 0.8−1.2‰ (Fig. 2a). Surface salinity more closely followed increasing bottom salinity at other sites (Fig. 2b-e). Upstream of Gravine Island, salinity at all depths remained negligible with McReynold's Lake experiencing only brief increases in salinity ≤ 0.5‰. Salinity remained ≤ 0.1‰ at Dennis Lake throughout the study.

Seasonal trends in water temperature were similar among sites, and temperature did not systematically vary along the downstream-upstream gradient (Fig. 3). Among years, days with temperature > 30°C occurred later in 2003 (mid-August−early September) than in both 2002 and 2004 (June−September). Peak summer temperatures were generally lower in 2003 (31.54°C) than in 2002 (33.83°C) and 2004 (32.91°C). Additionally, temperatures never rose above 30°C at Crab Creek or Dennis Lake in 2003, and the duration of temperature ≥ 30°C at other sample sites (D'Olive Bay, McReynold's Lake) was briefer than in 2003 (10−12 days) than in 2002 (22−72 days) and 2004 (21−34 days) at all sites.

Mean monthly discharge in 2003 was higher than in either 2002 or 2004 (Fig. 4a). Rather than decreasing through the spring and summer as was the case in 2002 and 2004, discharge remained higher from winter through summer in 2003. Although discharge began to decline throughout summer 2003, discharge levels similar to summer 2002 and 2004 did not occur until August. Also, 2002 and 2004 discharge increased at a higher rate during the fall than in 2003. Water-level patterns followed similar trends to those documented for discharge (Fig. 4b), except when water-levels decreased earlier during spring 2004 than 2002 and 2003.

Largemouth Bass Size

Size Indices. Few memorable (≥ 510 mm) and only one trophy size (≥ 630 mm) largemouth bass captured at Dennis Lake indicated that larger fish (≥ 2.3 kg) were uncommon throughout this system (Table 1). Most memorable or larger largemouth bass were found at upstream sites (Gravine Island, $N = 3$; McReynold's Lake, $N = 6$; Dennis Lake, $N = 3$). Only one memorable size fish was caught at both Bay Minette Bay and Crab Creek, and no memorable size fish were caught at D'Olive Bay.

Among-site comparisons in mean length. There was no consistent downstream-upstream pattern during 2002 ($F = 2.81$, $P < 0.05$) or 2004 ($F = 2.19$, $P = 0.053$), when among-site differences in mean length occurred (two-way ANOVA; site effect; Fig. 5). No differences among sites occurred in 2003 ($F = 0.96$, $P = 0.44$).

Temporal variation in mean length within-years. Mean length generally increased during late-winter/spring in 2002 and 2003, while timing varied more during 2004 (Fig. 5). Significantly greater (one-way ANOVA; month effect; all $P < 0.01$) mean length in 2002 (Duncan's Multiple Range Test; $P < 0.05$) occurred in March at Bay Minette Bay, Crab Creek, and McReynold's Lake and at Gravine Island during both October and March. In 2003, significantly greater (one-way ANOVA; all $P < 0.05$) mean length (Duncan's Multiple Range Test; $P < 0.05$) occurred in March at Bay Minette Bay, Crab Creek, Dennis Lake, and Gravine Island and during November at McReynold's Lake. Significantly greater (one-way ANOVA; all $P < 0.01$) mean length (Duncan's Multiple Range Test; $P < 0.05$) in 2004 occurred at Bay Minette Bay in February and March and Gravine Island in February and at Crab Creek, McReynold's Lake, and Dennis Lake in July.

Largemouth Bass Catch Rates

Among-site comparisons. In an effort to account for the large temporal variation in mean CPE values, we used ranked catch rates across sites on each date for comparisons (Fig. 6). There were differences among sites in all years (one-way ANOVA; site effect; all $P < 0.01$). Ranking patterns were similar across years, with McReynold's Lake, Bay Minette Bay, and Crab Creek typically ranked higher, and Dennis Lake, Gravine Island, and D'Olive Bay among lower ranking sites (Fig. 6). Repeated-measures split-plot ANOVA results also indicated significant among-site differences in mean CPE (Fig. 7; site effect), but only in 2002 ($F = 10.20$; $P < 0.01$) and 2004 ($F = 3.42$; $P < 0.05$). Differences (repeated-measures split-plot ANOVA; overall model) were not significant ($F = 1.32$, $P = 0.14$) in 2003. Similar to the average rank analysis, catch rates at McReynold's Lake, Bay Minette Bay, and Crab Creek were typically significantly higher than at Dennis Lake, Gravine Island, and D'Olive Bay.

Temporal variation within-years. Although sites experiencing more pronounced temporal variation were not similar across years (Fig. 7), timing of highest catch rates typically occurred during late winter or spring and lowest catch rates typically occurred throughout summer. In 2002, mean CPE differed by month (one-way ANOVA; month effect; all $P < 0.001$) at Bay Minette Bay, Crab Creek, and Dennis Lake. Significantly higher (Duncan's Multiple Range Test; $P < 0.05$) mean CPE occurred at Bay Minette Bay and Crab Creek during February and at Dennis Lake in both January and November; while significantly lower (Duncan's Multiple Range Test; $P < 0.05$) mean CPE occurred from May–August at Bay Minette Bay, March–August at Dennis Lake, and May–Oct at Crab Creek. No among-month differences (one-way ANOVA; month effect; all $P > 0.19$) in mean CPE were found for any site within 2003. In 2004, among-month differences in mean CPE (one-way ANOVA; month effect; all $P < 0.05$) occurred at D'Olive Bay, Crab Creek, McReynold's Lake, and Dennis Lake. Mean CPE was significantly higher (Duncan's Multiple Range Test; $P < 0.05$) during April at D'Olive Bay, McReynold's Lake, and Dennis Lake and during January at Crab Creek; while significantly lower (Duncan's Multiple Range Test; $P < 0.05$) mean CPE occurred from June–October at Crab Creek and during all months except April at D'Olive Bay, McReynold's Lake and Dennis Lake.

Temporal variation among-years. Mean CPE was generally lower throughout 2003 relative to 2002 and 2004 (Fig. 7). Mean CPE differed significantly among years (repeated-measures split-plot ANOVA, year effect) and was significantly lowest

(Duncan's Multiple Range Test; $P < 0.05$) at Crab Creek ($13.1 \cdot hr^{-1}$) during 2003. Although among-year differences were not significant (all $P \geq 0.09$) at Bay Minette Bay ($13.3 \cdot hr^{-1}$), McReynold's Lake ($17.1 \cdot hr^{-1}$), or Dennis Lake ($11.0 \cdot hr^{-1}$), lowest mean CPE also occurred during 2003 at these sites. Differences were not significant (repeated-measures split-plot ANOVA; overall model) at D'Olive Bay ($F = 1.77$, $P = 0.08$) or Gravine Island ($F = 1.22$, $P = 0.29$) and did not follow an among-year pattern similar to other sites.

Catch rates vs. environmental variability. Results from a 2DKS test (Fig. 8) indicated a threshold value of 2.71‰ for salinity ($D = 0.12$; $P = 0.0002$) and 16.0°C for temperature ($D = 0.09$; $P = 0.0002$). Hence, above these threshold values an increased probability of lower catch rates would be expected. An examination of our pooled data across years indicated that the combination of high salinity and low water temperature never occurred (Fig. 9).

Diet Composition

Within regions. A variety of identified prey types were consumed in all years (Tables 2-3). While blue crab, *Callinectes sapidus*, was the dominant prey species (by % total biomass) consumed downstream in all years, the dominant prey species consumed upstream varied among years. Dominant prey species consumed upstream were fat sleeper, *Dormitator maculatus* (2002); crayfish, Family Astacidae (2003); and red-spotted sunfish, *Lepomis punctatus miniatus* (2004).

Vertebrate consumption was typically greater than invertebrate consumption both upstream and downstream. Upstream (one-way ANOVA; prey effect; Fig. 11) in all years (all $P < 0.0001$) significantly more (Duncan's Multiple Range Test; $P < 0.05$)

vertebrates (2002 = 0.0310 $g \cdot g^{-1}$, 2003 = 0.0324 $g \cdot g^{-1}$, 2004 = 0.0361 $g \cdot g^{-1}$) were consumed than invertebrates (2002 = 0.0079 $g \cdot g^{-1}$, 2003 = 0.0073 $g \cdot g^{-1}$, 2004 = 0.0063 $g \cdot g^{-1}$). Downstream (one-way ANOVA; prey effect) in 2003 ($F = 7.70$, $P < 0.01$) and 2004 ($F = 20.93$, $P < 0.0001$) significantly more (Duncan's Multiple Range Test; $P < 0.05$) vertebrates (2003 = 0.0159 $g \cdot g^{-1}$, 2004 = 0.0238 $g \cdot g^{-1}$) were consumed than invertebrates (2003 = 0.0100 $g \cdot g^{-1}$, 2004 = 0.0111 $g \cdot g^{-1}$). No significant differences between prey types were found in 2002 ($F = 0.04$, $P = 0.84$).

Between-regions. Between-region (upstream vs. downstream) comparisons of mean per gram diet biomass ($g \cdot g^{-1}$) showed significantly greater (two-way ANOVA; region effect; Fig. 10) prey consumption upstream (2002: mean = 0.0211 $g \cdot g^{-1}$, 2003: mean = 0.0193 $g \cdot g^{-1}$) than downstream (2002: mean = 0.0074 $g \cdot g^{-1}$, 2003: mean = 0.0122 $g \cdot g^{-1}$) in 2002 ($F = 18.32$, $P < 0.0001$) and 2003 ($F = 12.48$, $P < 0.001$). Differences between upstream and downstream were not significant (two-way ANOVA; overall model; $F = 0.40$, $P = 0.90$) in 2004, although the trend was similar.

The percentage of the diets contributed by vertebrates differed consistently between regions for all years. Significantly more (two-way ANOVA; region effect; all $P < 0.01$; Fig. 11) vertebrates were consumed (Duncan's Multiple Range Test; $P < 0.05$) upstream (60−79%) than downstream (21−40%) in all years. However, the percentage of diets contributed by invertebrates did not consistently differ for all years. For invertebrate prey (two-way ANOVA; region effect; Fig. 11), significantly more ($F = 17.05$, $P < 0.0001$) invertebrates (Duncan's Multiple Range Test; $P < 0.05$) were consumed downstream (64%) than upstream (36%) in 2004. No significant between-region differences in invertebrate consumption occurred in 2002 (two-way ANOVA;

region effect; *F* = 1.50, *P* = 0.22) or 2003 (two-way ANOVA; overall model; F = 1.25, *P* = 0.28).

Between-region patterns relative to prey origin were not consistent across years (Fig. 12). Differences between regions in freshwater prey were not significant for any year (overall model; two-way ANOVA; all $P \geq 0.14$). During 2002 and 2003 (two-way ANOVA; region effect; all $P < 0.0001$), significantly more (Duncan's Multiple Range Test; $P < 0.05$) estuarine prey was consumed upstream (78−92%) than downstream (8−22%). Between-region differences were not significant for estuarine prey in 2004 (two-way ANOVA; overall model; *F* = 1.41, *P* = 0.20). For marine prey, differences between regions were not significant in 2002 (two-way ANOVA; overall model; *F* = 1.88, *P* = 0.07) or 2003 (two-way ANOVA; region effect; *F* = 2.94; *P* = 0.09). In 2004 (two-way ANOVA; region effect; *F* = 20.82, $P < 0.0001$), significantly more (Duncan's Multiple Range Test; $P < 0.05$) marine prey were consumed downstream (70%) than upstream (30%).

Temporal variation within-years. Although seasonal variation was significant (two-way ANOVA; season effect; Fig. 10) in 2002 (*F* = 2.81, $P < 0.05$) and 2003 (*F* = 4.09, $P < 0.01$) for all prey types consumed, the timing and location of greatest prey consumption was not similar. In 2002, system-wide prey consumption was significantly greater (Duncan's Multiple Range Test; $P < 0.05$) in fall and spring than in winter, and summer did not differ from other seasons. A significant interaction (two-way ANOVA; region*season effect; *F* = 5.02, $P < 0.01$) in 2003 indicated that season varied significantly (one-way ANOVA; season effect; *F* = 5.52, $P < 0.01$) upstream with significantly more (Duncan's Multiple Range Test; $P < 0.05$) prey consumed in winter and fall than in summer and spring. Seasonal differences (one-way ANOVA; overall model; $F = 1.46$, $P = 0.23$) were not significant downstream.

Seasonal variation was not consistent across years for both vertebrates and invertebrates consumed. Significant seasonal differences (two-way ANOVA; season effect; Fig. 11) were present only during 2002 ($F = 3.37$, $P < 0.05$) for vertebrate consumption; however a Duncan's Multiple Range Test ($P < 0.05$) did not indicate differences. No seasonal differences (two-way ANOVA; season effect) occurred in 2003 ($F = 1.44$, $P = 0.23$) or 2004 ($F = 1.87$, $P = 0.13$). Significant (two-way ANOVA; season effect; Fig. 11) seasonal variation ($F = 4.19$, $P < 0.01$) in invertebrate consumption occurred in 2002. System-wide consumption was significantly greater (Duncan's Multiple Range Test; $P < 0.05$) in spring than fall or winter, and summer did not vary from other seasons. Seasonal differences in invertebrate consumption were not significant in 2003 (two-way ANOVA; overall model; $F = 1.25$, $P = 0.28$). In 2004, a significant (two-way ANOVA; region*season effect; $F = 5.17$, $P < 0.01$) interaction indicated significant (one-way ANOVA; season effect; $F = 6.22$, $P < 0.001$) seasonal variation upstream with significantly greater (Duncan's Multiple Range Test; $P < 0.05$) consumption during fall than all other seasons, while differences were not significant downstream (one-way ANOVA; overall model; $F = 0.54$, $P = 0.65$).

There were no consistent seasonal patterns in mean per gram diet biomass relative to prey origin based on a consistent seasonal pattern. Seasonal variation of estuarine prey was not significant (two-way ANOVA; season effect; Fig. 12) in 2002 ($F = 0.67$, $P = 0.57$), but it was significant in 2003 ($F = 4.25$, $P < 0.01$) as was a significant interaction (two-way ANOVA; region*season effect; $F = 7.50$, $P < 0.001$). Seasonal variation was significant (one-way ANOVA; season effect) upstream ($F = 6.12$, $P < 0.001$), with significantly more (Duncan's Multiple Range Test; $P < 0.05$) estuarine prey consumed in winter and fall than summer and spring, while differences were not significant downstream (one-way ANOVA; overall model; $F = 1.27$, $P = 0.29$). System-wide seasonal variation in marine prey was significant (two-way ANOVA; season effect; Fig. 12) in 2003 ($F = 2.86$, $P < 0.05$), when significantly more (Duncan's Multiple Range Test; $P < 0.05$) marine prey was consumed in summer than spring, and fall and winter did not differ from other seasons. A significant interaction (two-way ANOVA; region*season effect) occurred for marine prey in 2004 ($F = 3.93$, $\mathrm{P} < 0.01$). Seasonal variation was significant upstream ($F = 5.70$, $P < 0.01$), where significantly more (Duncan's Multiple Range Test; $P < 0.05$) marine prey was consumed in fall than all other seasons. Differences in marine prey consumption were not significant downstream (one-way ANOVA; overall model; $F = 0.53$, $P = 0.66$).

Condition

Mean relative weight (mean Wr) was generally high for all sites in all years. Small fish (150−250 mm) had mean Wr ranging from 83−102 in 2002, 91−105 in 2003, and 90−106 in 2004. Larger fish (> 250 mm) had mean Wr ranging from 87−102 in 2002, 91−104 in 2003, and 88−102 in 2004.

In order to account for large temporal variation in mean Wr values, mean Wr was ranked across sites on each date for comparison. Average ranks indicated consistent and significant differences among sites for both small and large largemouth bass within all years (Fig. 13). Downstream sites (D'Olive Bay and Bay Minette Bay) generally ranked highest relative to upstream sites (McReynold's Lake and Dennis Lake).

Age, Growth, and Survival

Age-frequency and survival. For all years, few largemouth bass ≥ age-4 were collected (Fig. 14). Although survival was generally higher at upstream versus downstream sites (catch-curve regression; Fig. 15), survival for largemouth bass age-1 through age-5 generally remained low both downstream (36−52%) and upstream (45−57%) in all years (Table 4). The age-frequency pattern for Mobile-Tensaw Delta largemouth bass stocked in Monroe County Lake (Fig. 16a) resembled patterns obtained for largemouth bass from the Mobile-Tensaw Delta (Fig. 14). The increased numbers of age-4 and age-5 fish are likely due to higher recruitment of the original stocked fish (Fig. 15a). Catch-curve regression analysis (Fig. 16b) for ages 1−3 indicated an annual survival rate of 25% (Table 4).

Growth. Length-at-age for age-1 largemouth bass was significantly greater downstream than upstream (Bonferroni corrected t-tests: [2002: $t = 3.71$, $P < 0.001$], [2003: $t = 4.71$, $P < 0.0001$], [2004: $t = 3.02$, $P < 0.002$]). There were no other differences between downstream and upstream sites for other ages (Fig. 17a-c). When compared with 2004 mean length for largemouth bass from the Mobile-Tensaw Delta (Fig. 17c), mean length was significantly greater for largemouth bass ages 1−4 collected from Monroe County Lake in 2004 (Bonferroni corrected t-tests: [age-1: $t = -7.00$, $P < 0.0001$], [age-2: $t = -4.75$, $P < 0.00001$], [age-3: $t = -5.43$, $P < 0.0001$], [age-4: $t = -2.92$, $P < 0.01$], [age-5: $t = -2.73$, $P = 0.02$]).

The L_∞ parameter generated from the von Bertalanfy relationship indicated that maximum growth of largemouth bass throughout the Mobile-Tensaw Delta remained below 500 mm (Table 4). Therefore, time to reach memorable (510 mm) or trophy sizes

(630 mm) was not estimable as these sizes were outside the range of all von Bertalanfy relationships for largemouth bass from both the Mobile-Tensaw Delta and Monroe County Lake.

DISCUSSION

Although I demonstrated among-year variability for individual abiotic factors, the presence of multiple controlling factors at varying scales and possible interactions among these factors may have created difficulty in detecting the response of largemouth bass to individual factors. The lack of a downstream-upstream gradient pattern in mean size and catch rate indicated that salinity did not appear to drive these patterns as expected based on previous work (Swingle and Bland 1974, Tucker 1985). Seasonal patterns in catch rates and mean size occurred at some sites, but among-year variation in salinity, flow, and storm activity could have acted to obscure these trends. In addition, sampling gear bias could have occurred at increased salinity and flow. Despite the dynamic nature of this study system, the occurrence of a marine subsidy was indicated by consumption of marine-derived invertebrates by adults of all sizes, which tended to correspond with abiotic events. Generally high condition of largemouth bass throughout the Mobile-Tensaw Delta suggests that quality of food may be high and conditions are not necessarily crowded. Better condition among all sizes of fish and more rapid growth among smaller fish downstream relative to upstream may indicate a benefit to inhabiting downstream areas. However, overall low numbers of older fish, reduced survival, lack of a growth advantage after age-1, and an increase in growth potential when removed from coastal influences indicated that older adult coastal largemouth bass may not fully benefit from inhabiting coastal areas. I will now consider several of these specific findings relative to Mobile-Tensaw Delta largemouth bass and the abiotic environment in which they occur.

Abitoic factors

In my experience, salinity peaks and low flow occurred simultaneously each year, although the timing varied among years. Flow-related variability in salinity among years is likely to influence both the position and areal coverage of the estuarine boundary (Jassby et al. 1995, Meng and Matern 2001, Kimmerer 2002, Peterson 2003). In addition, hurricane activity varied among years (Appendix 2), further increasing uncertainty in an already highly variable abiotic environment by displacing saltwater and marine inhabitants far inland and leading to widespread vegetation die-offs and fish kills (David L. Armstrong, Jr., personal communication). Such environmental variability certainly influences estuarine populations and ecological processes operating there (Crecco and Savoy 1985, Garvey et al. 2000, Rakocinski et al. 2000, Peterson et al. 2004).

Fluxes of nutrients or prey in aquatic systems are often thought to be generated by abiotic forces as well as movement of consumers across habitat boundaries (Polis et al. 1997). Rather than actively moving across the freshwater-marine ecosystem boundary, however, largemouth bass are more likely to become surrounded by increasing salinity as the position of the estuarine ecotone shifts during portions of each year, thereby allowing them to gain access to resources from the marine ecosystem. While the potential for ecosystem interactions may exist for freshwater species in estuarine habitats through such means, freshwater-marine linkages are still not well-represented beyond anadromy and catadromy. As such, ideas proposed for linked ecosystems do not address less mobile organisms.

Mean Size

Abiotic forces are also thought to influence the distribution of largemouth bass in coastal systems. As an explanation for low average weight (0.24 kg) and capture of few large largemouth bass, an earlier study (Swingle and Bland 1974) suggested that largemouth bass ($\geq$ age-1) moved upstream during increasing salinity and remained there, resulting in crowded conditions. Meador and Kelso (1990b) further suggested that juvenile coastal largemouth bass may be restricted to downstream areas during increasing salinity due to predation risk. Largemouth bass are not the only large predators in the Mobile-Tensaw Delta. Other predators, such as gar species *Lepisosteus spp.*, bowfin *Amia calva*, southern flounder *Paralychthis lethostigma*, red drum *Sciaenops ocellatus*, American alligator *Alligator mississippiensis*, bald eagle *Haliaeetus leucocephalus*, osprey *Pandion haliaetus carolinensis*, and cormorants *Phalacrocorax spp.*, etc. were frequently sighted (personal observation). While larger largemouth bass were slightly more common upstream than downstream in the Mobile-Tensaw Delta, differences among sites did not indicate a significant increase in mean total length from downstream-upstream as might be expected if fish systematically moved upstream to escape increased salinity. Current work has shown that downstream areas are valuable as both spawning and nursery areas (Peer et al. 2006), and larger and older (up to age-5) fish were never entirely absent from our most downstream sites. However, potential predators were commonly observed throughout our study area, and were not limited to downstream areas. In addition, bass of all sizes throughout the study area were found to have open wounds or punctures, missing body parts, and scarring perhaps caused by predation attempts. While largemouth bass typically attain larger size relative to their prey within their first year and become dominant predators in freshwater systems (Heidinger 1975, Olson 1996), the potential for increased predation on largemouth bass inhabiting large coastal systems has not been addressed and the influence of predator-mediated movement at increasing salinity is less known.

Catch rates

Higher catch rates were found when salinity was less than 2.7‰. Although salinity ≥ 5‰ has been suggested to initiate movement to upstream, freshwater areas (Meador and Kelso 1989), movement away from increasing salinity has not been directly linked to reduced catch rates. During a movement study in the same area of the Mobile-Tensaw Delta, Norris et al. (2005; Chapter 3) found that while salinity did not rise above 2‰, population-wide movements of largemouth bass due to salinity did not occur. Also, Keup and Bayless (1964) found freshwater fish in greatest abundance at a salinity of < 2.63‰ and uncommon in salinity above 10.50‰. It should also be noted that use of electrofishing gear in estuarine or high conductivity systems may reduce sampling efficiency (Reynolds 1996). As such, the potential for salinity-related movement and thresholds initiating this movement remains unclear.

Catch rates were generally higher when temperatures were below 16.0°C during late fall through early spring. Higher catch rates in this study tended to occur from winter into spring, while lower catch rates typically occurred during summer. Seasonal trends in abundance of largemouth bass in freshwater systems have been explained by localized (< 1 km) movement patterns due to spawning, summer temperatures, or in response to prey availability (Savitz et al. 1983, Mesing and Wicker 1986, Bain and Boltz 1992, Wildhaber and Neill 1992). Similar seasonal trends in movement have also been suggested for largemouth bass in low-salinity systems (Meador and Kelso 1989, Norris et al. 2005). Hence, these seasonal movements may be more localized due to largemouth bass moving to deeper water, beyond the range of electrofishing gear.

The timing of peak salinity and temperature may influence catch rates and possibly other response variables. For instance, similarly timed salinity and temperature peaks may interact to reduce catch rates more than salinity and temperature peaks that are off-set from one another. However, due to reduced efficiency at increased salinity and the lack of a high salinity-low temperature combination in our study area, we cannot completely identify the interacting effects of salinity and temperature. Flow may also influence the movement of coastal largemouth bass (Meador and Kelso 1989, Norris et al. 2005), and movement responses may differ depending on the magnitude, relative timing, and co-occurrence of flow with other abiotic factors.

We also found that catch rate patterns may be influenced by variation in river discharge. Among-years, catch rates were lowest in 2003 at Bay Minette Bay, Crab Creek, McReynold’s Lake, and Dennis Lake. This was in contrast to our expectation of increased catch rates based on lower temperature and salinity that occurred in 2003. Catch rates may have been reduced due to increased discharge and water levels, particularly at upstream, forested sites, where the forest floor was flooded during high water. Largemouth bass may have moved into these newly inundated, but difficult to sample, shallow areas, returning to previous locations after water levels retreated (Raibley et al. 1997, Norris et al. 2005).

Within the downstream-upstream gradient, flow-related habitat differences among sites may also affect catch rates. For instance, consistently low ranking catch rates occurred during all years at Dennis Lake, Gravine Island, and D'Olive Bay. These sites were either in a main river channel or had an open connection to a main river channel. Sites with relatively higher catch rates (McReynold's Lake, Bay Minette Bay, Crab Creek) tended to be more closed to flow and not directly connected to any main river channel. Flows in main channel versus off-channel habitats have been shown to affect distributions and abundances of species found in riverine systems (Dettmers et al. 2001) and may explain why catch rates of largemouth bass did not vary strictly along a downstream-upstream gradient.

Diets

Largemouth bass inhabiting coastal areas have been found to consume invertebrate prey (Colle et al. 1978, Lorio 1982). Meador and Kelso (1990b) found that invertebrates contributed > 50% by number of coastal largemouth bass diets. We also found a similar pattern in invertebrate consumption through numerical and percent total biomass diet analysis for largemouth bass at downstream sites. However, mean per gram diet biomass showed a different result, in which vertebrates were the dominant prey consumed by largemouth bass throughout the Mobile-Tensaw Delta in all years. Biomass estimates are better when comparing among prey types of varying weight structure (Bowen 1996), and mean per gram biomass estimates can further account for variation in consumer size. Despite this, invertebrates, particularly those of marine origin, were consistently present in adult largemouth bass diets from throughout the

Mobile-Tensaw Delta, which indicates an energetic subsidy from the marine environment.

Mixing of prey from marine and freshwater ecosystems along an estuarine gradient has been documented, and the ratio of freshwater to marine species has been shown to increase with decreasing salinity (Peterson and Ross 1991). However, marine species are typically better able to tolerate decreasing and fluctuating salinity as they move up-estuary than freshwater species are able to tolerate increasing and stabilizing salinity levels as they move down-estuary (Peterson and Ross 1991). This suggests that the freshwater-marine linkage remains strong even when salinity decreases along the downstream-upstream gradient and further stresses the importance of considering this interaction in freshwater species like largemouth bass that inhabits tidal freshwater and oligohaline environments.

Influxes of marine and estuarine invertebrates upstream were highly variable across years, presumably due to variability in freshwater inflows. The magnitude and timing of the salinity peak during mid-summer 2002 may have been such that increased availability of estuarine prey types occurred upstream. Despite a reduced and delayed salinity peak in 2003, the salt wedge was well-established up to Gravine Island, similar to other years, and may explain the presence of increased estuarine prey in upstream areas during fall and winter. A late summer salinity peak along with increased hurricane activity (e.g., Hurricane Ivan) during fall 2004 may have displaced marine prey upstream and could explain increased marine prey consumption in upstream relative to downstream sites during fall.

Meador and Kelso (1990b) suggested high condition (mean Wr = 83−152) for coastal largemouth bass. Largemouth bass throughout the Mobile-Tensaw Delta generally were in good condition (mean Wr > 85), but condition was increased downstream relative to upstream for all sizes of largemouth bass. In freshwater systems, establishing target ranges for high condition can be dependent on various factors (e.g., seasonality, reproduction, availability of high quality food, uncrowded conditions, fish health, etc.), and one target range for largemouth bass with high condition has not been determined, although Wr > 85 typically signifies good condition (Blackwell et al. 2000). In addition, marine influences on condition are not known.

Because our sampling schedule should have accounted for monthly variation, increased Wr downstream relative to upstream may indicate a benefit to inhabiting downstream habitats, possibly stemming from prey type consumed (e.g., marine vs. freshwater, invertebrates vs. vertebrates) on condition. It has been proposed that consumption of invertebrates may cause allocation of energy toward growth differently than consumption of vertebrates, resulting in reduced length relative to weight (Meador and Kelso 1990b). This could suggest that current relative weight equations, based on length-weight relationships for freshwater largemouth bass (Wege and Anderson 1978), may not be adequate for determining condition of coastal populations of largemouth bass.

Age, growth, and survival

Abiotic factors can influence age, growth, and survival in fish populations (Crecco and Savoy 1985, Rutherford et al. 1995, Gutreuter et al. 1999, Rypel et al. 2006). Peak summer temperatures were ≥ 30°C at most sites, especially in 2002 and 2004. Reduced growth in largemouth bass may result when temperature exceeds 27°C, which is their energetic optimum when food is not strongly limited (Coutant 1975, Rice et al. 1983). Although higher discharge and increased water levels in spring can increase availability of shallow, off-channel habitat to adults for spawning, poorly timed or rapidly-fluctuating spring water levels may reduce nest success, YOY growth, and recruitment to age-1 (Miranda et al. 1984, Goodgame and Miranda 1993, Garvey et al. 2000). These effects could eventually lead to reduced adult survival. While effects of salinity on largemouth bass are not fully understood, previous studies suggest that even low levels of salinity can influence largemouth bass populations. Experimental findings suggest largemouth bass show signs of physiological stress, increased energetic cost, and reduced reproductive ability as salinity rises above 4‰, (Tebo and McCoy 1964, Meador and Kelso 1990a). An ontogenetic shift in salinity tolerance may also occur given that adults do not fair as well as juveniles once salinity approaches 10‰ (Susanto and Peterson 1996). Largemouth bass have been found in higher salinity (17.5‰; Swingle and Bland 1974), but mortality over prolonged periods (120 days) of salinity ≥ 12‰ has been shown experimentally (Meador 1988). Mortality as a result of increasing salinity likely did not occur in our study area as surface salinity never exceeded 10‰. In the presence of these various abiotic forces, physiological stress likely affected metabolic processes with population-level consequences.

Although largemouth bass were longer at age-1 downstream versus upstream, no differences were found for older fish (see also Peer et al. 2006). However, this differs from findings reported by Meador and Kelso (1990b), where reduced growth was evident by age-1 fish. While Peer et al. (2006) found that invertebrates no longer dominated age-0 diets after transitioning to piscivory at approximately 100 mm, a complete transition to piscivory did not occur as macroinvertebrates were commonly consumed by adults. Prey consumption patterns of adult coastal largemouth bass in the Mobile-Tensaw Delta may differ from juveniles such that the early growth advantage in length at downstream sites is not maintained in older fish.

Reduced growth has been reported for coastal compared to freshwater largemouth bass (Lorio 1982, Tucker 1985, Meador and Kelso 1990b). In a Louisiana study, where salinity as high as 12‰ was reported, Meador and Kelso (1990b) showed increased growth of coastal relative to freshwater largemouth at age-3, but these results were from instantaneous growth rates in back-calculated total length. They also documented shorter back-calculated length-at-age for coastal relative to freshwater fish between age-1 and age-2. In comparison to growth rates provided by Meador and Kelso (1990b) from other studies, shorter length-at-age did not appear to occur until age-4 and age-5 for Mobile-Tensaw Delta largemouth bass relative to freshwater fish. In addition, mean lengths-at-age also appeared to be greater in our study than for coastal populations from other studies reported by Meador and Kelso (1990b). In a North Carolina study (Guier et al. 1978), coastal largemouth bass were reported to experience increased growth as salinity increased across river systems, but the range of salinity largemouth bass were exposed to was relatively low (0-5‰). Effects of salinity on growth may depend on the salinity level largemouth bass are exposed to and may even vary among systems. It should also be taken into consideration that Meador and Kelso (1990b) did not report growth rates for fish older than age-5 from other studies or older than age-4 from their own study and no explanation for the lack of older fish was provided. Few largemouth bass older than age-4 were present in our study, and back-calculated mean lengths-at-age may not have been representative for fish older than age-4. Low numbers of older fish were also reflected in annual survival rates for both downstream (36−52%) and upstream sites (45−47%), given that freshwater largemouth bass can have annual survival rates > 70% (e.g., Brown and Maceina 2002). Although growth differences of older fish between upstream and downstream in the Mobile-Tensaw Delta were not evident in our study, lower annual survival and a subsequent paucity of older fish throughout the Mobile-Tensaw Delta may lead to a scarcity of large-sized (> 2.3 kg) largemouth bass in coastal systems more than has been previously indicated.

Significantly greater growth occurred for largemouth bass from the Mobile-Tensaw Delta when living in the freshwater Monroe County Lake relative to growth in the Mobile-Tensaw Delta. Hallerman et al. (1986) found that while there were growth differences between largemouth bass in the Mobile-Tensaw Delta versus upriver, genetic differences based on isozymes were minimal, suggesting that reduced largemouth bass growth in the Mobile-Tensaw Delta was due more to an environmental effect than a genetic effect. Clearly, in the Mobile-Tensaw Delta, there is an environmental effect given greater growth potential of Mobile-Tensaw Delta largemouth bass in Monroe County Lake than in the Mobile-Tensaw Delta itself.

Alternately, annual survival remained low for largemouth bass from both the Mobile-Tensaw Delta and Monroe County Lake. While many prior studies have suggested that coastal largemouth bass exhibit reduced size-at-age relative to their freshwater counterparts (Tucker 1985, Meador and Kelso 1990b), none of these studies have included annual survival rates of coastal largemouth bass or an explanation for the paucity of fish older than age-4, and growth rate comparisons between freshwater and coastal largemouth bass are limited in the primary literature (Meador and Kelso 1990b). Growth and survival comparisons of latitudinally similar coastal and freshwater populations would be ideal. However, largemouth bass from the Mobile-Tensaw Delta are northern largemouth bass (Norgren et al. 1986), and stocking of Florida largemouth bass throughout much of the southeastern United States presented an additional challenge for such comparisons. Despite this, the potential for reduced survival in the absence of coastal influences may provide some preliminary evidence for a genetic effect, rather than simply an environmental effect.

Management Implications

Interactions between freshwater and marine ecosystems create a dynamic, highly uncertain abiotic environments. As such, influences from both upstream freshwater input and downstream marine input in the Mobile-Tensaw Delta are likely. However, current fisheries management practices for freshwater fishes in the Mobile-Tensaw Delta are similar to those of inland reservoirs. While the largemouth bass fishery is a recreationally and economically important fishery in this system, this species is also ecologically important and can serve as an example of how humans can affect ecosystem interactions and the role of a species within that ecosystem.

In addition to natural abiotic variability, more than 30 inland reservoirs are located on rivers upstream of the Mobile-Tensaw Delta. Much of our study area is located within protected wildlife management areas, but upstream effects from development, water use, and reservoir operations may increase demand on aquatic resources and alter the flow regime downstream in the Mobile-Tensaw Delta. Within the Mobile-Tensaw Delta, downstream portions of the system are subject to increased development as well as proposed plans to alter the causeway spanning the lower end. Many of these changes could modify the extent to which freshwater and marine ecosystems interact within this system. Hence, it is not clear whether reservoir management practices are effective when applied to a coastally influenced system experiencing cumulative local and upstream anthropogenic effects.

Use of size indices and condition equations commonly applied in management of purely freshwater systems, particularly reservoirs and small impoundments, have been relatively successful in managing largemouth bass populations. However, current size and condition indices may not appropriately account for marine influences and perhaps the specific biology of coastal largemouth bass. Hence conclusions drawn from these analyses may need to be re-evaluated.

Conclusions and Future Directions

Additional work should be done to link the potential for reduced abundance and mean size with increased salinity and confirm whether some upper salinity threshold exists to initiate movement into upstream, freshwater areas. Due to a consistent invertebrate component in adult coastal largemouth bass diets, future work should address how environmental conditions create shifts in consumption from vertebrate to invertebrate prey. Evaluating profitability of various combinations of prey (marine versus freshwater, invertebrate versus vertebrate) may improve our understanding of potential differences in allocation of energy toward growth between freshwater and coastal largemouth bass, which can further confirm the applicability of current Wr equations for coastal populations. Additional work may further investigate the potential mechanisms creating the disparity in growth between age-1 and older largemouth bass through identifying potential benefits from prey fluxes. Evolutionary adaptations by a freshwater species to dynamic environmental conditions (e.g., salinity, temperature, flow, prey, predation, etc.) in coastal systems may have given rise to low annual survival and may point to a “live fast, die young” life history strategy. However, more consideration should be given to reduced longevity and low survival rates in order to identify the mechanisms resulting in this reduced growth pattern in coastal largemouth bass. Also, additional research on the differences in overall growth patterns as well as incremental growth between coastal and freshwater largemouth bass could better define growth differences. Modeling approaches in general, and bioenergetics modeling in particular, combined with experimental approaches may be necessary to build on patterns found in this field study in order to better define the effects interacting abiotic variables have on population characteristics of largemouth bass.

While the dynamic nature of the estuarine ecotone no doubt incurs its own set of challenges in defining transfer of resources, better defining energy and material subsidies could allow broader application for freshwater-marine linkages. Despite limited application (e.g., anadromous and catadromous species) for freshwater-marine linkages, we believe this to be conceptually valuable in addressing the complexity of interactions between freshwater and marine ecosystems and ultimately leading to improved management. More work and collaboration across research and ecosystem boundaries could improve applicability to freshwater-marine linkages, which may be imperative given the potential for increasing demands on upstream water resources to put further strain on the already impaired flow regime within the Mobile-Tensaw Delta

III. MOVEMENT OF LARGEMOUTH BASS (MICROPTERUS SALMOIDES) IN THE MOBILE-TENSAW RIVER DELTA, ALABAMA: A MULTI-APPROACH STUDY

INTRODUCTION

Study of largemouth bass (*Micropterus salmoides*) has been quite extensive in a wide array of freshwater systems, due in large part to their popularity as a recreational sportfish (Nack et al. 1993, Markham et al. 2002). This research has produced a large volume of information regarding both the ecology and management of largemouth bass (hereafter referred to as bass) in freshwater systems (Garvey et al. 2000, Philipp and Ridgway 2002). However, little is known about bass in the numerous coastal systems they inhabit.

The bass present in the oligohaline and upstream portions of estuarine systems along the mid-Atlantic and Gulf coasts can be exposed to periodic salinity (Meador and Kelso 1990b, Peterson and Meador 1994). Throughout their range in coastal systems, reduced size and low catch rates of large bass have been documented both scientifically (Tucker 1985, Meador and Kelso 1990b) and by anglers. For bass tournament anglers reporting catches from 2002 and 2003, 1,743 angler-hours were required to catch a bass > 2,268 g in 2002, and no bass of this size were caught in 3,498 angler-hours in 2003 in the Mobile-Tensaw Delta as compared to an average from these two years statewide in Alabama of 519 angler-hours to catch a bass > 2,268 g (Nichols and McHugh 2002, Haffner et al. 2003). Linking these population trends to coastal influences has motivated many studies (Colle et al. 1976, Guier et al. 1978, Hallerman et al. 1986, Meador and Kelso 1990a,b, Susanto and Peterson 1996, Peer 2004). However, the degree to which salinity directly or indirectly (e.g., marine/estuarine derived prey and predators) affects coastal bass habitat choice and movement remains unclear. As in other coastal systems, this question is made more complex by anglers moving bass (Richardson-Heft et al. 2000, Krause 2002).

The openness, and increased spatial scale of coastal systems relative to most lentic, freshwater systems potentially allows individuals to represent one well-mixed population or several distinct sub-populations. Numerous studies on bass movement in small lakes or reservoirs (Savitz et al. 1983, Mesing and Wicker 1986, Bain and Boltz 1992, Wildhaber and Neill 1992) indicate localized, seasonal movements (< 1 km) corresponding with spawning or changing temperature. The more diverse, interconnected habitats found in riverine systems, especially coastal systems with salinity in downstream areas, may cause fish to move more readily; however, our understanding of the effects of such coastal influences on population mixing remains limited. When salinity reached 5‰ in a Louisiana study and no fish were found, the suggestion was that bass moved upstream to freshwater areas (Meador and Kelso 1989). Experimental evidence has indicated that bass prefer salinities ≤ 3‰ (Meador and Kelso 1989) and experience mortality when held at salinities ≥ 12‰ for prolonged periods of time (Meador and Kelso 1990a). While an individual bass was collected at 17.5‰ (Swingle and Bland 1974), freshwater fish typically dominate catches at lower salinities (< 1‰, Swingle and Bland 1974; < 2.63‰, Keup and Bayless 1964). Therefore, the absolute salinity needed to initiate movement to upstream freshwater locations remains unconfirmed and may depend on processes affecting movement of salinity within systems. In addition, the rate of salinity fluctuations combined with the interaction of salinity with other variables (e.g., temperature, etc.) is likely to affect the physiological tolerances of organisms to salinity (Meador and Kelso 1989, Wheatley 1988).

In this study, we hypothesized that the movement of adult bass in the Mobile-Tensaw Delta would be affected by salinity. We expected movement of adult bass to be greater in downstream areas than in upstream areas as the salinity gradient developed. We used three approaches to assess movement of bass related to increasing salinity; external tagging of bass to identify movement within and among sample sites, acoustic telemetry to identify movement at one downstream and one upstream location, and acoustic and external tagging of bass at two tournament release sites to evaluate dispersal from tournament release areas.

METHODS

Study Site

The Mobile-Tensaw Delta (hereafter referred to as the Mobile Delta) comprises 8,224 ha between the confluence of the Alabama and Tombigbee rivers and the head of Mobile Bay and forms a network of rivers, creeks, bays, lakes, wetlands, and bayous (Armstrong et al. 2000). It is the fourth largest river delta in the United States (Tucker 1985) and spans a length of nearly 55 km and a width up to 15 km. During our study, salinity peaks (1 meter depth) in the Mobile Delta reached as high as 9.3‰ in the most downstream portions, while upstream portions remained fresh. Tidal influence (average tidal range < 0.5 m) on saltwater intrusion is minimal, except at maximum amplitude (Schroeder 1978). Habitat ranges from tidal freshwater marshes downstream to hardwood forests upstream.

External Tagging

We sampled a downstream-upstream salinity gradient using six fixed sites along the lower, eastern portion of the Mobile Delta (Fig. 18a). Sites extended approximately 33 km from just south of I-10 and the US 90/98 Causeway north to I-65. Monthly electrofishing (pulsed-DC) at each site, starting in July 2002 and ending in December 2004, included boom and prod-pole electrofishing (Smith-Root DC Electrofisher, 7.5 GPP, 7,500 W). Boom electrofishing consisted of two 15-min transects in nearshore waters < 2 m deep, while prod-pole electrofishing consisted of three 10-min transects associated with shoreline areas.

Bass (≥ 200 mm) were measured (nearest mm TL), weighed (nearest g), externally tagged (N = 1,025; Guy et al. 1996) with T-bar anchor tags (FD-68B; FLOY Tag, Inc.), and released where they were collected. Individually numbered tags also included a phone number to enable anglers to report their recaptures. Although no reward system was used, there is an active bass fishery in the Mobile Delta with anglers voluntarily reporting tagged bass.

Acoustic Telemetry

One upstream site (Dennis Lake; Fig. 18c) and one downstream site (Bay Minette Bay; Fig. 18d) were selected for the release of acoustic transmitter tagged bass. The primary habitat in Bay Minette Bay was a shallow, heavily vegetated bay about 3 km from the nearest main river channel, while the dominant habitat in Dennis Lake consisted of a smaller river channel with sparse aquatic vegetation about 0.6 km to the nearest main river channel. In previous years, the salinity at 1 meter depth approached 5‰ at Bay Minette Bay and never reached detectable concentrations at Dennis Lake.

Bass (N = 40) were tagged and released in a spring (March 2003) and fall (October 2003) phase. For larger individuals (N = 32), a 16 X 63 mm, 8 g, 14-month minimum tag (CT-82-2, SONOTRONICS, Inc.) was implanted, and a 9.5 X 28 mm, 2.5 g, 60-day minimum tag (IBT-96-2, SONOTRONICS, Inc.) was implanted for smaller bass (N = 8). Tags never weighed more than 2% of bass wet weight in air (Winter 1996).

Each individual was measured, weighed, and externally tagged as described previously. Surgery and anesthesia techniques for tag implantation were similar to Winter (1996). Each surgery was completed within 5 minutes, and the gills were irrigated during surgery. Tagged bass recovered for at least 30 minutes and were released at a central location in each site (Fig. 18c,d).

Fish were located using a hand-held, DH-2 directional hydrophone and USR-5W digital receiver (30–85 kHz; SONOTRONICS, Inc.) approximately monthly during day hours. Spring-released fish were sampled from March 2003−December 2004, and fall-released fish were sampled concurrently with spring-released fish from October 2003−December 2004. Although the approximate expected ranges for the smaller tags were 500 m and the larger tags were 1,000 m in seawater, locations were selected conservatively to compensate for habitat complexity (i.e., bends in channels, channel or embayment mouths, or aquatic vegetation). The hydrophone was rotated three times, with each rotation at a different frequency (low, medium, and high) within the range of tag frequencies (70−80 kHz). If a tag signal was detected, the individual tag code was first identified and then the receiver frequency was adjusted to within 1−2 kHz of the tag frequency to maximize the signal received. Specific locations were isolated by triangulation. An equally loud signal in all directions indicated a fish location, and a GPS coordinate (GPS 12 Personal Navigator, Garmin, Inc.), surface temperature, salinity, and total depth were recorded for each fish.

Tournament Release Site

Acoustic Telemetry. A downstream location (USS Alabama; Fig. 18e), previously used for tournament releases, was selected as a release site, where the potential return of bass above the Causeway could be identified. Bass (N = 5) were electrofished in April 2004 from Bay Minette Bay, located upstream of the Causeway, and implanted with acoustic transmitter tags. After surgery and recovery, tagged bass were transported to the USS Alabama and released (Fig. 18e). Salinity was recorded at the release point. Two days after release, we returned to the USS Alabama and surrounding area and listened for the presence of signals. Fish were tracked for three months following release, which corresponded with the monthly tracking for Bay Minette Bay and Dennis Lake.

External tagging. Bass weighed-in at a tournament (15 May 2004) at Live Oak Landing on the Tensaw River (Fig. 18b) were placed in large holding tanks adjacent to tagging teams. Salt was added to all tanks to reduce osmotic stress on fish. All tournament caught bass (N = 362) were measured, weighed, externally tagged, and placed in recovery tanks. All fish were processed in less than 3 hours and were released directly into the Tensaw River immediately adjacent to the weigh-in and tagging location (Fig. 18b).

We electrofished (as described above) 4, 13, and 23 days post-release covering the downstream and upstream shorelines of the Tensaw River adjacent to the release location (total distance radius = 1 km; total pedal time = 100−120 min). Total numbers of tagged and untagged bass and GPS coordinates and tag numbers of recaptured individuals were also recorded.

Data Analysis

For bass relocated with the acoustic telemetry approach, monthly means for abiotic variables were calculated. Individual distances moved for bass relocated using acoustic telemetry or recaptured individuals from the tournament tagging were calculated using Terrain Navigator software (MAPTECH, Inc.) with GPS coordinates taken in the field. Mean distances by month were also calculated for bass relocated at Bay Minette Bay and

Dennis Lake and by post-release sampling date for tournament recaptures. Two-way ANOVAs with interaction effects ($P < 0.05$) were used to test for statistical differences both spatially and temporally. Due to limited data on smaller adults through time, data from both size categories were combined for analysis.

RESULTS

External Tagging

During three years of standard sampling at six sites, we tagged and released a total of 1,025 bass (Table 5). Of these, 62 were recaptured (49 in our sampling; 14 reported by anglers), with total recaptures at any one site generally < 10 bass. While most recaptured bass were released (77−100% across years), the remainder were kept for age-and-growth analysis. Only two bass were recaptured more than once (both released and recaptured in Crab Creek). Most bass (86−100% across years) were recaptured where they were released. Only two bass were found to move between sampling sites. Both of these fish were originally tagged and released at Crab Creek in April 2003 and recaptured in Bay Minette Bay in May 2003, representing an estimated movement (minimum total distance) of 15.8 km in ≤ 37 days.

Though most bass (63−100% across years) were recaptured within 3 months following release, recaptures of bass tagged in previous years increased during the study. Months since initial release ranged from 1−18 months for recaptured bass across years, with 6 individuals recaptured in 2004 between 10−18 months after initial release. No bass released in 2002 were recaptured in later years, but seven bass recaptured in 2004 were initially released in 2003. Most fish were recaptured during February through May, which included months just prior to or during spawning in both 2003 (64%) and 2004 (66%).

Although angler reporting of tagged bass remained low throughout the study (Table 5), these reports included one fish caught in McReynold's Lake (May 2004) and released in a private fishing pond and another fish tagged and released at D'Olive Bay in August 2003 and recaptured in the vicinity of Pascagoula, Mississippi in January 2004. No movement between sample sites was found through angler reporting.

Acoustic Telemetry

Total lengths of larger bass released at Bay Minette Bay in Spring 2003 (N = 8) ranged from 320 to 452 mm (mean ± 1 SD = 378 mm ± 48.8), and in Fall 2003, they ranged from 340 to 530 mm (N = 8, mean ± 1 SD = 425 mm ± 60.8). Larger bass tagged at Dennis Lake in Spring 2003 (N = 8) ranged in size from 359 to 448 mm (mean ± 1 SD = 388 mm ± 28.7) and from 352 to 425 mm (mean ± 1 SD = 380 mm ± 29.0) in Fall 2003 (N = 8). Smaller bass released at Bay Minette Bay in Spring 2003 (N = 2) were 265 mm and 272 mm (mean ± 1 SD = 269 mm ± 4.9) and 299 mm and 304 mm (mean ± 1 SD = 302 mm ± 3.5) in Fall 2003 (N = 2). Smaller bass tagged at Dennis Lake in Spring 2003 (N = 2) were 240 mm and 241 mm (mean ± 1 SD = 241 mm ± 0.7) and 285 mm and 290 mm (mean ± 1 SD = 288 mm ± 3.5) in Fall 2003 (N = 2).

A total of 155 individual relocations were made during April 2003 through December 2004 (Dennis Lake = 84, Bay Minette Bay = 71). We relocated all bass from each site and release phase at least one time, except for fall-released fish at Bay Minette Bay. Only 70% of these fish were relocated at least once. Essentially, all bass were relocated at least once in Dennis Lake, and 86% were relocated at least once in Bay Minette Bay. Relocations during any one monthly sample varied from 0−70% in Bay Minette Bay and Dennis Lake. In Bay Minette Bay, the percent of relocations by month were highest in the months immediately after the spring-release (70% in April 2003) and the fall-release (40% in December 2003 and February 2004). Highest percentages of relocations by month (50%) from the spring release were not isolated to a specific time (April 9, April 26, October, and December 2003) in Dennis Lake, while the highest percentage (70%) of monthly relocations occurred immediately after the fall release (October 2003). Although the percentage of relocations decreased to 0% during May 2003 at both Dennis Lake and Bay Minette Bay, percentages rebounded in the following months at both sites.

Salinity peaked at our downstream site, Bay Minette Bay, in August 2002 (4.9‰), November 2003 (1.5‰), and September 2004 (1.7‰), and remained fresh at our upstream site, Dennis Lake. In March 2003, bass were released at Bay Minette Bay in freshwater at a surface water temperature of 19.7°C, and bass were released at Dennis Lake in freshwater at 18.7°C. In October 2003, bass were released at Bay Minette Bay in 1.4‰ salinity and 26.2°C, while bass in Dennis Lake were released in freshwater at 24.9°C.

Spring-released bass (Fig. 19a) were relocated at Bay Minette Bay when salinity was present in October (N = 3) and November (N = 4) of 2003. Mean salinities for spring-released bass in Bay Minette Bay were 1.0‰ (range = 1.0‰-1.1‰) in October 2003 and 1.4‰ (range = 0.3‰-1.9‰) in November 2003. Only one spring-released bass (0.3‰) was relocated in October 2004 during increased salinities. Similarly, fall-released bass (Fig. 19b) were relocated during increased salinities at Bay Minette Bay in October 2003 (N = 3) at mean salinities of 0.7‰ (range = 0.2‰-1.0‰) and in November 2003 (N

= 2) at mean salinities of 1.6‰ (no range). In October 2004, only one fall-released bass (0.2‰) was present with increased salinity.

Only two bass were found to move to areas with lower salinity when ambient salinity increased. As salinities increased in Bay Minette Bay during 2003, one spring-released bass moved 1.1 km upstream toward Bay Minette Creek, the main freshwater inflow. This fish moved from 1.1‰ salinity in October 2003 to 0.3‰ salinity in Bay Minette Creek by November 2003 (month of peak salinity). After salinity declined, this fish returned to its previous location and remained there. The other fish moved 1.3 km toward Bay Minette Creek immediately after its fall release when salinities were 1.4‰ to a salinity of 0.2‰ at its relocation site. This bass was relocated only one other time in February 2004 moving farther upstream into Bay Minette Creek.

Peak temperatures ranged from 30.7°C (August 2003) to 32.7°C (August 2002, July 2004) in Bay Minette Bay, and peak temperatures were 28.9°C (September 2003), 31.8°C (July 2004), 32.4°C (August 2002) in Dennis Lake. Peak surface water temperatures were lowest at both sites in 2003 and occurred one month later in Dennis Lake than in Bay Minette Bay.

A significant month x site interaction ($F = 13.32$, $P < 0.01$) indicated that mean temperatures at relocation points for spring-released bass were significantly higher in Bay Minette Bay than Dennis Lake during April, June, and July of 2003 (Fig. 19c). In 2004, mean temperatures at relocation points for spring-released bass were significantly higher in Bay Minette Bay during February, March, May, July, and October than in Dennis Lake. Likewise, a significant month x site interaction ($F = 7.68$, $P < 0.01$) indicated that fall-released bass were found in significantly higher temperatures at Bay Minette Bay than Dennis Lake during October 2003 and March, July, October, and December 2004 (Fig. 19d).

Although no significant month x site interaction (F = 1.41, P = 0.18) was found for mean total depth, both the month (F = 1.90, P = 0.047) and site effects (F = 6.53, P = 0.01) were significant for spring-released bass (Fig. 19e). Spring-released bass in Bay Minette Bay (mean = 76.8 cm) were relocated in shallower water than in Dennis Lake (mean = 125.2 cm). Conversely, significant differences (F = 4.39, P = 0.045) between sites for fall-released fish (Fig. 19f) indicated that bass were relocated in Dennis Lake (mean = 87.5 cm) at shallower depths than in Bay Minette Bay (mean = 178.6 cm).

While the Bay Minette Bay habitat type was primarily represented by a shallow, heavily vegetated bay, all locations of bass at this site occurred along the edges of the less vegetated, deeper side channels. In general, dense vegetation is minimal at Dennis Lake, and bass in Dennis Lake tended to be associated with fallen trees, submerged brush piles, or root wads immediately adjacent to the deeper channel.

Although mean total distances did not differ by site [spring (F = 0.82, P = 0.66); fall (F = 0.77, P = 0.65)] or month [spring (F = 0.01, P = 0.94); fall (F = 0.91, P = 0.35)] for largemouth bass released in the spring (Fig. 19g) or fall (Fig. 19h) and despite a greater distance to the main river channel at Bay Minette Bay (3 km) than Dennis Lake (0.6 km), a subset (N = 3) of bass from Bay Minette Bay moved to the Blakeley River (Fig. 18d), the nearest main river. One spring-released fish was relocated three times as it progressed into the main river (November 2003 – February 2004) and was last relocated moving downstream in the Blakeley River (3.6 km from release). The second fish (fall-released) moved upstream upon reaching the Blakeley River (5.3 km from release) and was relocated there two times (February, May 2004). A third fish (fall-released) moved toward the Blakeley River (December 2003; 2.4 km from release), then returned upstream, and crossed Bay Minette Bay (Fig. 18d) to a location in Bay Minette Creek (February 2004; 3.5 km from previous location) where it remained for the duration of the study. Only one fish (spring-released), from Dennis Lake (Fig. 18c) moved to the Tensaw River (2.7 km from release), the nearest main river, and was not found there until July 2003 where it stayed for the remainder of the study.

Three fish were also relocated by Maurice F. Mettee (Geol. Survey of Alabama, pers. commun.) during June 2004. Of the fish not in our routine sampling path, one fish, originally released in Dennis Lake, was relocated 21.3 km upstream, and the other fish, originally released in Bay Minette Bay, was relocated upstream in the Blakeley River (8.7 km from the release site). The third of these fish was previously located during our routine sampling and was described above as the only fish moving into the Tensaw River from Dennis Lake.

An effect from angling was also indicated by this approach. One angler reported recapturing a spring-released bass in Bay Minette Bay. A fall-released fish at Dennis Lake appeared to be in the live well of an angler while we were tracking it in October of 2003. October was the first tracking trip after the fall release, and no other relocations for this fish were obtained after this.

Tournament Release Site

Five bass ranging in size from 354 to 404 mm TL (mean ± 1 SD = 370 mm ± 19.9) were tagged and released at a downstream site, the USS Alabama Battleship Memorial Park. Surface and bottom salinity levels in Bay Minette Bay at the time of capture were both 0.1‰, while surface and bottom salinity levels at the USS Alabama release site were 4.5‰ and 10.4‰, respectively. Two days post-release, three bass were detected in the area of the battleship downstream of the 90/98 Causeway and I-10 overpass. One fish was detected near the release site, a second fish was detected downstream, and a third fish was detected in an easterly direction across the Tensaw River. In the following months, no fish were located upstream or downstream of the battleship until a final attempt in April 2005 resulted in the relocation of one bass 451 m upstream of the release point but still downstream of the 90/98 Causeway and I-10 overpass. This fish was first relocated moving downstream of the release location in April 2004.

At the Team Jesus bass tournament on 15 May 2004 at Live Oak Landing, upstream of Dennis Lake and I-65, we tagged and released 362 bass. In our post-tournament electrofishing, 36, 13, and 2 tagged bass were collected 4, 13, and 23 days respectively after the tournament. Although mean distance moved by bass did not differ significantly, a general trend toward increasing distance (mean minimum distance) away from the release location through time (mean ± 1 SE; day 4 = 402 m ± 44.33; day 13 = 349 m ± 70.82, and day 23 = 610.5 m ± 158.8) occurred. While distance moved by bass was significantly ($F = 8.01$, $P < 0.01$) greater in the upstream direction (mean ± 1 SE = 533 m ± 60.21) than in the downstream direction (mean ± 1 SE = 328 m ± 41.53) from the release point, a greater proportion of bass moved downstream (67%) than upstream (33%) of the release location.

Subsequently, anglers reported recapturing 8 bass from this tournament. Two anglers recaptured bass around the release location while fishing for another tournament.

One released their recaptured bass at another tournament weigh-in location 14.2 km downstream of the release location. The other released a bass 32.5 km upstream at another tournament release location. Another bass was recaptured by an angler ~ 20 days post-release in the mouth of Dennis Lake (10.2 km from the release location). Two other fish were also recaptured near the tournament release, but no involvement in a tournament was indicated. Another three fish were recaptured in nearby water bodies though movements to these locations would have been larger in terms of river miles.

DISCUSSION

Coastal bass exhibit an apparent reduced growth rate with few individuals reaching large size (Tucker 1985, Meador and Kelso 1990b). To understand the mechanisms that cause this pattern, it is necessary to determine movement patterns of bass in response to environmental stress (e.g., increasing salinity) associated with coastal systems and identify if movement could affect observed patterns via mixing of sub-populations (Copeland and Noble 1994, Jackson et al. 2002).

Bass move among habitats in response to many environmental factors including food availability (Fish and Savitz 1983, Savitz et al. 1983), avoidance of low dissolved oxygen (Wildhaber and Neill 1992), temperature preferences (Warden and Lorio 1975), and vegetation density (Savino and Stein 1989, Kilgore et al. 1989). Previous studies suggest that bass also move to preferred spawning areas that may differ from their choice of habitat during other periods (Mesing and Wicker 1986, Nack et al. 1993, Richardson-Heft et al. 2000).

Unlike smaller, freshwater systems, where one movement pattern tends to predominate in relation to an environmental stress, bass populations in the Mobile Delta were found to exhibit three different movement patterns at downstream sites, (1) remain in deeper side channels directly connected to shallow bay; (2) move upstream with increasing salinity; (3) move into or toward main river channel. While salinity remained low throughout the telemetry study, other coastal influences associated with downstream sites (e.g., habitat variation, greater influence from marine/estuarine prey or predators) may also influence bass movement at downstream sites in the absence of high salinity.

Rather than migrating to spawning locations in embayments and creek mouths as shown for bass in the tidal freshwater portions of the Hudson River and the Chesapeake Bay (Nack et al. 1993, Richardson-Heft et al. 2000), one subset of the acoustic tagged fish at Bay Minette Bay and most of the tagged fish at Dennis Lake remained in these protected habitats (i.e., channels) throughout the year, instead of moving strictly during the spawning season. As has been suggested in freshwater systems, longer residence by bass in these channels may be due to a combination of protection from wind and wave action (Mesing and Wicker 1986), immediate access to deeper water during increased temperatures (Warden and Lorio 1975), higher quality or more abundant food resources concentrated within a smaller area (Fish and Savitz 1983, Savitz et al. 1983), or less dense aquatic vegetation allowing increased foraging access (Savino and Stein 1989, Killgore et al. 1989) lacking in the shallower and heavily vegetated, but predominant bay habitat.

It has been hypothesized that bass move upstream to freshwater during increased salinity (Swingle and Bland 1974, Meador and Kelso 1989, 1990b). Although we were able to relocate bass during increased salinity at Bay Minette Bay, peak salinities only approached 2‰ and may not have been high enough to initiate movement to lower-salinity waters. Only a small subset of tagged bass (one from each release phase) made upstream movements (but only 1.1-1.3 km) as salinity increased at Bay Minette Bay. While one bass returned to its previous location after salinity declined, the other bass continued moving upstream until February 2004, when it was relocated for the last time. Other studies also indicated reduced catches of freshwater fish at low salinities (Keup and Bayless 1964, Swingle and Bland 1974). Therefore, future work during years of higher salinity should continue to identify whether a salinity threshold exists to initiate bass movement in the Mobile Delta.

Despite the increased distance to a main river channel at Bay Minette Bay (3 km) relative to Dennis Lake (0.6 km), a third subset of bass (2/release phase) moved to the main river channel at Bay Minette Bay. Distances moved by bass from the Bay Minette Bay release point ranged from 2.4−8.7 km. Because distances moved for this subset of tagged fish were greater than the typical distances moved (< 1 km) by bass in freshwater systems, angler displacement may be a possible explanation. However, only one bass moved to the closer main river channel at Dennis Lake, indicating either differences in angler use of areas in the Mobile Delta or other factors driving this movement pattern for a portion of the population. Hence, separating the effects of anglers from other environmental factors would be useful in advancing our understanding of movement patterns of bass in coastal systems.

The lack of relocations both downstream and upstream during high water levels in May 2003 suggested movement by bass outside of the detection area. Our ability to relocate bass among the fallen trees, submerged brush piles, and root wads along the channel edges and along vegetated channel edges during normal water levels in the months immediately prior to and after high water levels suggested that bass had indeed moved out of the channels, but their quick return indicated a lack of any extensive movements away from the area. Unfortunately, our ability to detect the sonic tags in the forested shallows was greatly limited by lack of access to these areas and the obstruction of signals by the forested or vegetated edges.

Higher temperatures at downstream relative to upstream sites may be due to the shallow bay habitat found at Bay Minette Bay and the shaded riverine habitat in Dennis Lake− habitats typical of downstream and upstream locations in this system. With temperatures above 27°C for 4−5 months of the year at Bay Minette Bay and 3−4 months of the year at Dennis Lake, restricted activity, particularly during foraging, may contribute to reduced growth rates of adult bass (Rice et al. 1983). Less efficient conversion of food to growth at smaller sizes was found in age-0 bass from the Mobile Delta and Florida populations compared to Wisconsin populations at higher temperatures as indicated through bioenergetics modeling and was thought to be the result of local adaptation to the extreme high temperatures they experience at southern latitudes (Slaughter et al. 2004). Innovative bioenergetics modeling including habitat choice, movement, and salinity as parameters along with food and temperature in simulations will permit a better energetic understanding of how these variables interact to effect growth differences.

While salinities never reached the level needed to force bass to move at sites above the Causeway, surface salinity did approach 5‰ when we released acoustically tagged bass at the USS Alabama release site. Initial movements of these fish (2 days post-release) did not indicate movement upstream of the release location. Because none of the fish were relocated > 2 days post-release, this indicated that bass had moved out of the area, but upstream movement was not confirmed. One fish was relocated 1 year after release just upstream of the release site but below the I-10 and Route 90/98 overpasses.

A study of tournament displacement by Ridgway (2002) found few bass transplanted > 8 km from their capture sites in Rideau Lake, Ontario returned and those displaced within that range could take up to one year to return to their original capture site. However, another study of bass movement in the tidal freshwater and oligohaline portions of the Chesapeake Bay indicated a return to capture sites over distances of 21 km (Richardson-Heft et al. 2000). None of the tagged bass released at the battleship site returned to the site of their capture (16 km) up to 1 year after release. Further research is needed on the effects (e.g., mortality or movement away from salinity) of release into areas of increased salinity for bass originating from upstream freshwater areas. Improved knowledge of common capture locations relative to tournament release locations is needed to address the potential for return to a capture site in the Mobile Delta and the potential localized effect of release site distance from capture site on bass populations in this system.

Although most recaptured bass concentrated within a 0.5 km radius of the upstream tournament release longer (4 days = 58%; 13 days = 77%) than a study of post-tournament stockpiling (< 7 days) of bass in the Chesapeake Bay (Richardson-Heft et al. 2000), complete dispersal outside this radius occurred by 23 days post-release. This may indicate an increased length of time for stockpiling of bass as a result of tournament activity in the Mobile Delta. In addition, relative to the potential effects of angler displacement, our externally tagged bass were generally recaptured at their release sites. Given the time range (1−18 months) between release and recapture and the high rate of recaptures during spawning, these fish may be making localized movements out of the range of our sampling methods. Compared with recaptures of externally tagged bass that were originally captured, released, and typically recaptured in the same local area, bass transplanted by tournament activity generally moved away from the release site indicating an attempt to either return to an old home range or establish a new home range. Therefore, continued research on the effects of tournament practices in concentrating bass around release sites may further assist our understanding of the population effects of these potentially extensive re-distributions of fish throughout this system.

It was evident from each of our research approaches that fish are often displaced by anglers. External tags were reported by anglers from bass that were released in other systems (e.g., freshwater fishing pond, coastal waters surrounding Pascagoula, Mississippi). Acoustic telemetry provided evidence for the presence of a tagged fish in an angler live-well. Both acoustic telemetry (21.3 km) and tournament tagging (32.5 km) indicated large-scale movements outside of our routine sampling areas. Some anglers reported the use of recent tournament release locations as favorite fishing sites for later tournaments, which lends further support to the potential for continuous re-distribution of concentrations of fish to various tournament release locations throughout the Mobile Delta.

CONCLUSIONS

Several types of movement patterns were observed in bass in downstream portions of the Mobile Delta, while movement patterns of bass in the upstream portions remained less variable throughout the study. Although increasing salinity appeared to directly influence bass movement in only a couple of instances, likely due to low salinity experienced during this study, other coastal influences (e.g., habitat variation, marine/estuarine derived prey and predators) may have contributed to these downstream-upstream differences in movement patterns. Our results suggest that some potential for population mixing exists within downstream areas, while bass populations from upstream areas remained relatively isolated from downstream areas. As angler effects were evident for all approaches, more research is needed to separate the effects of coastal influences and angler displacement on bass and to improve our understanding of the contribution these factors may have in isolating or mixing bass populations within such coastal areas.

Table 1. Annual (2002-2004) Proportional Stock Density (PSD; ≥ 300 mm), Relative Stock Density-Preferred (RSD-P; ≥ 380 mm), Relative Stock Density-Memorable (RSD-M; ≥ 510 mm), Relative Stock Density-Trophy (RSD-T; ≥ 630 mm) for largemouth bass from seven sites.

Sample Sites	PSD	RSD-P	RSD-M	RSD-T
2002				
Dennis Lake	47	16	1	1
McReynold's Lake	38	14	1	0
Gravine Island	38	5	1	0
Crab Creek	30	4	0	0
Bay Minette Bay	56	13	0	0
D'Olive Bay	30	5	0	0
Below Causeway	38	5	0	0
2003				
Dennis Lake	51	17	3	0
McReynold's Lake	43	14	1	0
Gravine Island	34	7	0	0
Crab Creek	30	6	1	0
Bay Minette Bay	36	12	1	0
D'Olive Bay	36	13	0	0
2004				
Dennis Lake	52	19	0	0
McReynold's Lake	50	23	3	0
Gravine Island	52	16	1	0
Crab Creek	41	8	0	0
Bay Minette Bay	38	11	0	0
D'Olive Bay	50	16	0	0
Combined Mean Total				
Dennis Lake	50	17	1	0
McReynold's Lake	43	17	2	0
Gravine Island	41	9	1	0
Crab Creek	34	6	0	0
Bay Minette Bay	43	12	0	0
D'Olive Bay	39	11	0	0

Table 2. Total biomass (%) of identified fish based on all identified prey types consumed by largemouth bass (2002-2004) at downstream (DS) and upstream (US) sites in the Mobile-Tensaw Delta. Prey were classified as marine (M) or estuarine (E) if they depended on these environments to fulfill part of their life cycle, while prey with limited salinity tolerance were assigned as freshwater (F) prey.

	2002		2003		2004	
Prey Identification	DS	US	DS	US	DS	US
Fish						
Banded topminnow (F)	-	-	-	-	0.05	-
Bay anchovy (M)	0.75	0.11	0.30	0.01	-	0.08
Bluegill (F)	0.61	-	2.12	13.72	4.57	2.90
Blue-spotted sunfish (F)	-	-	-	-	0.20	0.28
Brown bullhead (F)	-	-	1.01	-	-	-
Chain pickerel (F)	-	-	9.95	0.52	0.04	0.22
Channel catfish (F)	5.75	-	-	0.47	-	-
Clown goby (E)	0.12	0.18	-	0.19	0.62	0.51
Coastal shiner (F)	-	-	-	-	0.10	-
Unidentified drum (F)	-	-	-	-	0.16	-
Eel (M)	-	0.23	-	3.77	-	-
Fat sleeper (E)	-	40.84	-	-	-	-
Gambusia spp. (F)	0.05	-	-	-	-	-
Golden shiner (F)	0.46	0.54	-	-	0.59	-
Golden topminnow (F)	-	-	-	-	-	0.06
Gulf killifish (E)	-	-	-	-	0.04	0.22
Gulf menhaden (M)	-	-	7.54	-	0.68	1.33
Herring (M)	-	-	0.06	-	-	-
Hogchoker (E)	-	-	0.02	-	-	-
Inland silverside (F)	-	-	0.07	-	1.93	-
Unidentified jack (M)	-	-	-	-	0.37	-
Largemouth bass (F)	5.45	-	3.12	0.74	0.05	3.61
Pipefish (E)	1.23	0.02	0.72	0.46	0.21	-
Pirate perch (F)	-	-	-	-	-	1.14
Pugnose minnow (F)	-	-	-	-	-	0.07
Redear sunfish (F)	-	8.01	3.73	0.19	2.74	4.37
Red-spotted sunfish (F)	0.79	1.11	9.72	11.99	4.78	24.25
Rainwater killifish (E)	0.42	0.74	1.11	0.08	0.19	0.23
Sand seatrout (M)	0.66	-	-	-	-	-
Sharptail (highfin) goby (E)	-	-	-	7.96	2.46	-
Sheepshead minnow (E)	-	-	-	-	0.13	-
Silverside shiner (F)	-	-	0.74	1.59	-	0.61
Skipjack herring (F)	-	-	-	-	-	1.93
Speckled worm eel (E)	-	-	0.02	-	-	-
Spot (M)	0.80	-	-	-	0.46	-
Swamp darter (F)	-	-	-	-	-	0.05
Threadfin shad (F)	-	5.56	-	-	-	0.18
Warmouth sunfish (F)	-	-	1.31	3.43	8.02	-
Weed shiner (F)	-	-	-	-	-	0.09
Western starhead topminnow (F)	-	0.77	0.18	-	-	0.06

Table 3. Total biomass (%) of identified non-fish prey based on all prey consumed by adult largemouth bass (2002-2004) from downstream (DS) and upstream (US) sites in the Mobile-Tensaw Delta (M = Marine, E = Estuarine, F = Freshwater).

	2002		2003		2004	
Prey Identification	DS	US	DS	US	DS	US
Other Vertebrates						
Greater siren (E)	-	-	-	-	-	29.26
Green tree frog (E)	1.43	-	-	-	2.41	-
Snake (E)	-	28.01	-	-	-	-
Crustacean Invertebrates						
Amphipod (E)	-	-	0.04	0.01	0.07	0.01
Blue crab (M)	73.53	7.96	37.00	12.75	54.07	16.53
Crayfish (F)	-	2.17	0.07	25.91	2.02	8.29
Grass shrimp (E)	-	-	1.59	2.33	4.63	1.37
Larval shrimp (M)	-	<0.01	<0.01	0.04	-	-
Mud crab (M)	7.46	3.46	19.88	3.15	6.71	1.21
Mysid shrimp (M)	-	-	<0.01	<0.01	0.01	0.02
White shrimp (M)	0.38	0.01	0.41	0.07	0.69	0.23
Zooplankton (E)	-	-	<0.01	<0.01	<0.01	<0.01
Other Invertebrates						
Arachnid (E)	-	-	0.22	-	0.37	<0.01
Worms (E)	-	0.29	0.01	<0.01	0.07	<0.01
Gastropod (E)	-	-	0.33	0.16	0.31	-
Hirudinea (E)	-	-	0.09	0.10	0.07	0.28
Insects (E)	0.10	<0.01	0.06	0.04	0.10	0.24
Mussel (E)	-	-	-	-	0.24	-
Miscellaneous Organic/Inorganic						
Artificial lure	-	-	-	0.54	0.34	0.44
Seed	-	<0.01	-	-	0.01	0.02
Rock	-	-	-	-	0.07	-
Wood	-	-	-	-	0.03	-

Table 4. Estimated von Bertalanfy parameters for bass of all ages and survival rates estimated from catch curve regression analysis for largemouth bass age-1 through age-5 at downstream and upstream sites from 2002-2004 and from age-1 through age-3 at Monroe County Lake in fall 2004.

Year	Survival	L_∞	k	t
2002				
Upstream	0.45	401.6	-0.58	0.17
Downstream	0.36	400.6	-0.50	0.15
2003				
Upstream	0.50	433.8	-0.36	0.28
Downstream	0.46	449.1	-0.26	1.12
2004				
Upstream	0.52	434.9	-0.42	0.27
Downstream	0.57	457.9	-0.36	0.21
Monroe County Lake	0.25	488.0	-0.46	-0.29

Table 5. Numbers of bass externally tagged, released, and recaptured in sampling (labeled 'AU Recapture' within the table) and by anglers for all sample sites and years.

	Numbers of Bass			
Sites	2002	2003	2004	Site Total
Dennis Lake				
Tagged/Released	12	73	80	165
AU Recapture	0	3	3	6
Angler Recapture	0	1	1	2
McReynold's Lake				
Tagged/Released	38	82	74	194
AU Recapture	0	0	5	5
Angler Recapture	0	2	2*	4
Gravine Island				
Tagged/Released	29	27	64	120
AU Recapture	0	1	5	6
Angler Recapture	0	0	3	3
Crab Creek				
Tagged/Released	48	66	75	189
AU Recapture	1	4[†]	8[†]	13
Angler Recapture	0	0	0	0
Bay Minette Bay				
Tagged/Released	35	99	122	256
AU Recapture	0	4[‡]	8	12
Angler Recapture	0	3	1	4
D'Olive Bay				
Tagged/Released	28	27	46	101
AU Recapture	0	2	3[§]	5
Angler Recapture	0	1	1[£]	2
Combined Site Total				
Tagged/Released	190	374	461	1,025
AU Recapture	1	14	32	47
Angler Recapture	0	7	8	15

*Only recapture location known for one bass. Release location was unknown, because complete tag number not available.

[†] Two bass were recaptured twice each (N = 1 in 2003, N = 1 in 2004).

[‡] Two recaptured bass counted in Bay Minette Bay were initially released in Crab Creek.

[§] Only recapture location of one bass known. Release location was unknown, because no number was on tag.

[£] One bass was recaptured in Pascagoula, Mississippi but initially released in D'Olive Bay where it was counted.

Figure 1. Map of the Mobile-Tensaw Delta, Alabama, USA including sample sites from downstream to upstream (D’Olive Bay, Below Causeway, Bay Minette Bay, Crab Creek, McReynold’s Lake, and Dennis Lake).

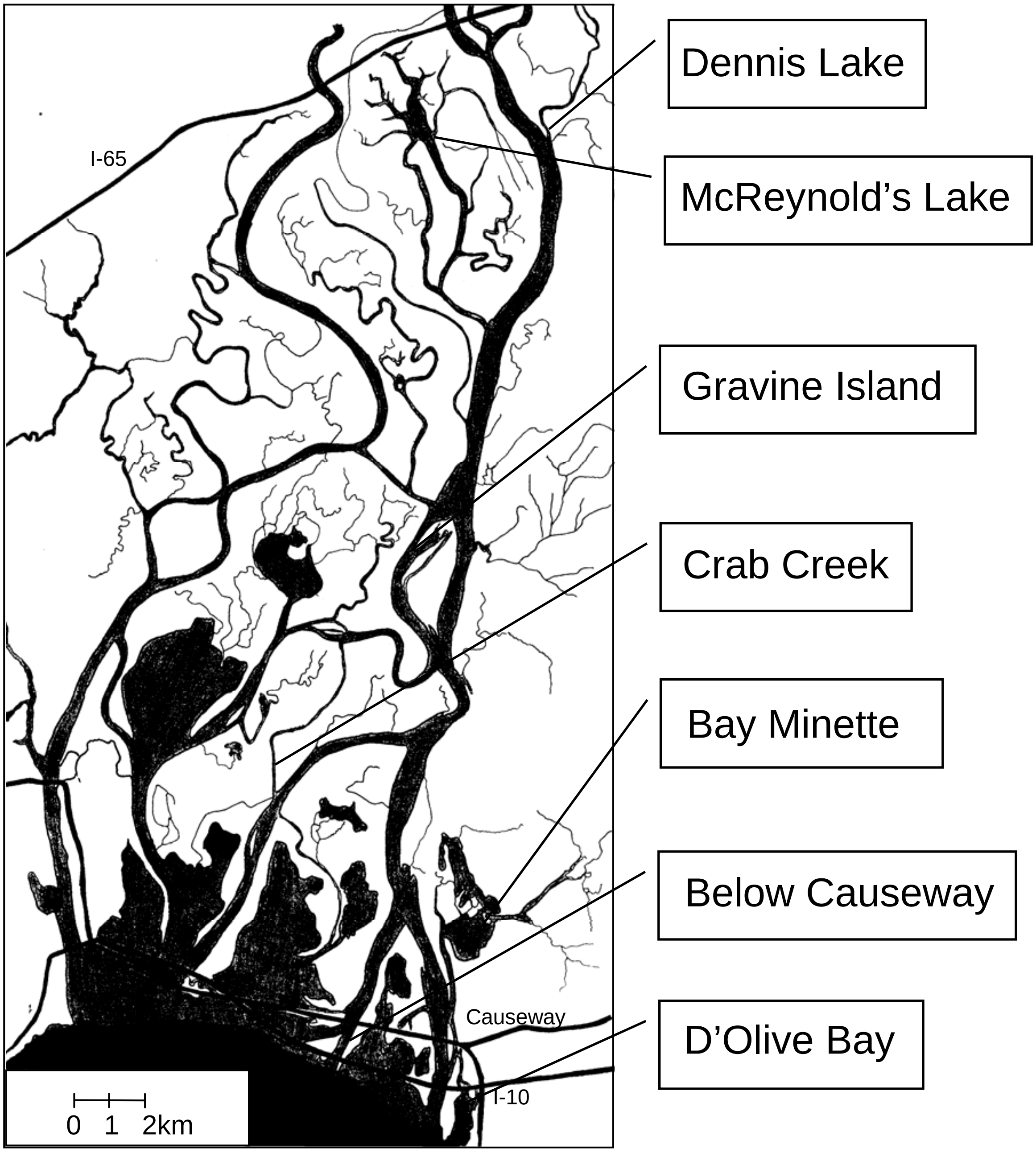

Dennis Lake
McReynold’s Lake
I-65
Gravine Island
Crab Creek
Bay Minette
Below Causeway
Causeway
D’Olive Bay
I-10
0 1 2km

Figure 2. Mean monthly surface and bottom salinity values (‰) at (a) Gravine Island, (b) Crab Creek, (c) Bay Minette Bay, (d) Below Causeway, and (e) D'Olive Bay. McReynold's Lake and Dennis Lake were not included because salinity was negligible or did not occur at these sites.

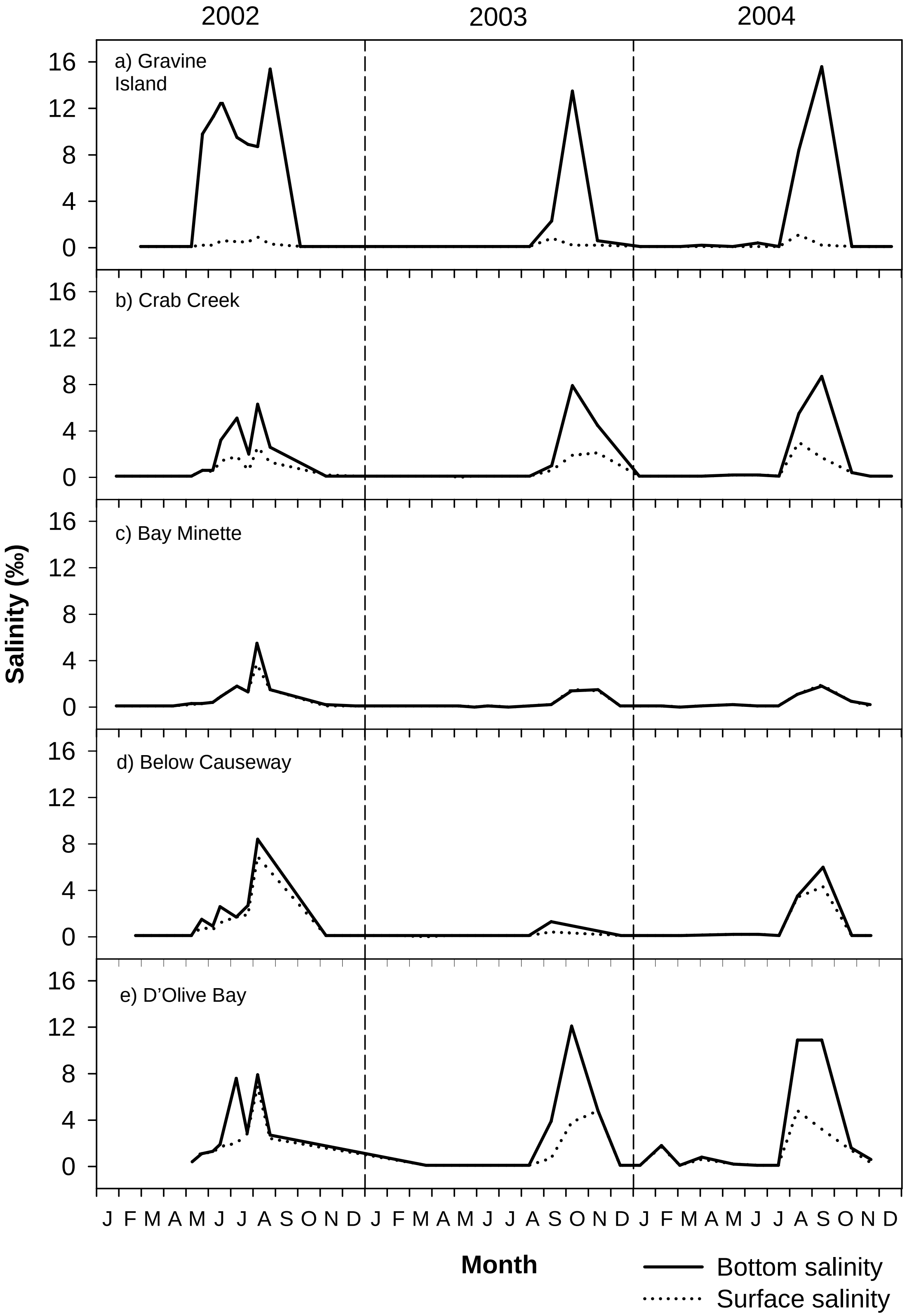

2002
2003
2004
a) Gravine Island
b) Crab Creek
c) Bay Minette
d) Below Causeway
e) D'Olive Bay
Salinity (‰)
0
4
8
12
16
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
Month
Bottom salinity
Surface salinity

Figure 3. Mean daily temperature (°C) from temperature loggers at six sample sites during 2002-2004. Continuous temperature data were not available at Bay Minette Bayduring 2003 and 2004, at Gravine Island during 2002 and 2003, and at McReynold's Lake during 2002 due to loss of loggers.

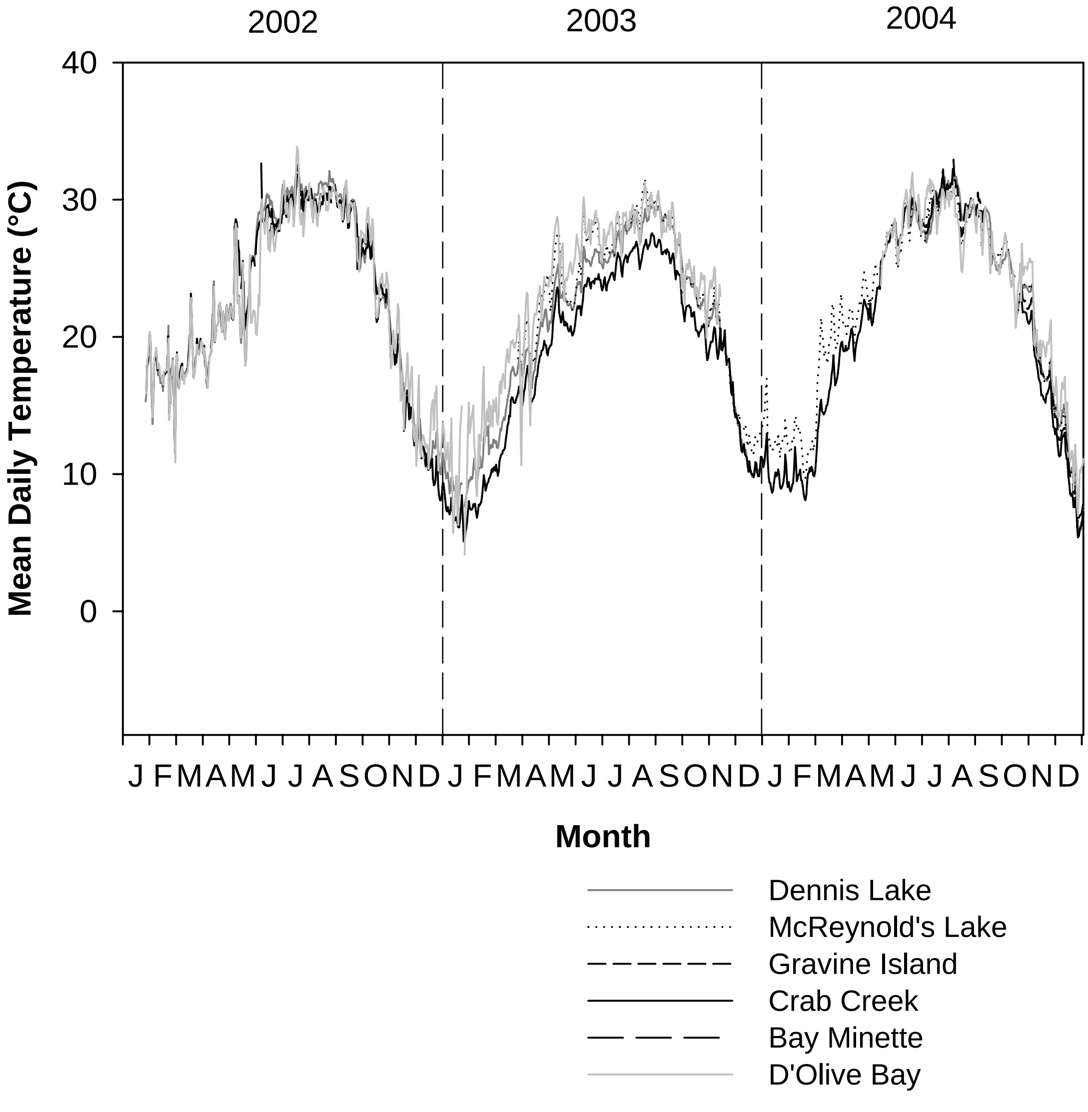

2002
2003
2004
40
30
20
10
0
Mean Daily Temperature (°C)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
Month
Dennis Lake
McReynold's Lake
Gravine Island
Crab Creek
Bay Minette
D'Olive Bay

Figure 4. (a) Mean monthly stream-flow (cfs) estimated by combining values from USGS stream gages on the Alabama River at Claiborne Lock and Dam (#02428400) and Tombigbee River at Coffeeville Lock and Dam near Coffeeville, AL (#02469761) for 2002-2004. Data were not available for October 2003. (b) Mean daily gage height (m above sea level) from 2002-2004 based on data from the USGS stream gage at Barry Steam Plant on the Mobile River at river mile 31.0 near Bucks, AL (#002470629).

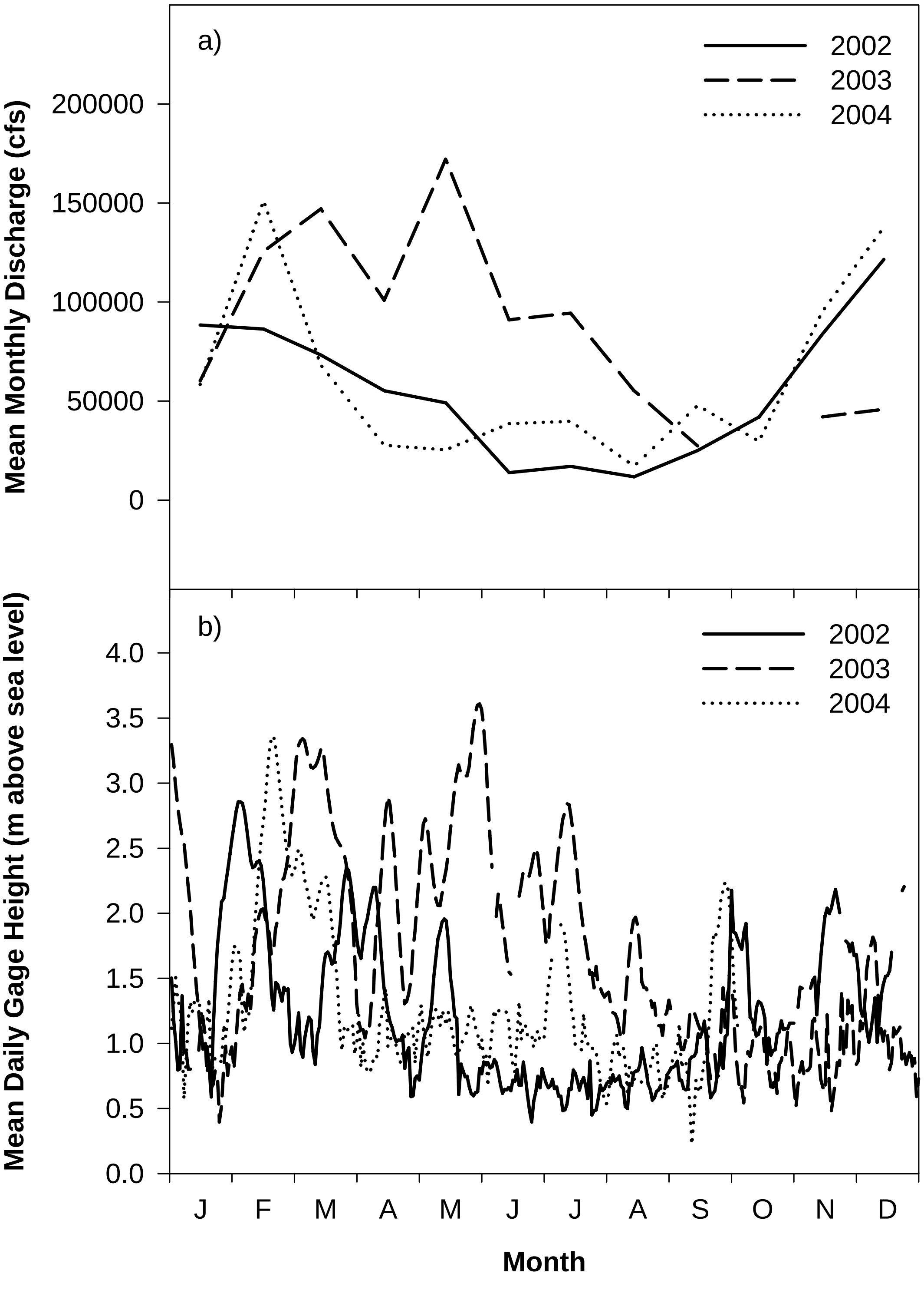

a)
2002
2003
2004
Mean Monthly Discharge (cfs)
200000
150000
100000
50000
0
b)
2002
2003
2004
Mean Daily Gage Height (m above sea level)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure 5. Monthly mean total lengths (mm) of largemouth bass by site for (a) 2002, (b) 2003, and (c) 2004 in the Mobile-Tensaw Delta. Site differences are indicated within each graph (two-way ANOVA, Duncan’s Multiple Range Comparison, α = 0.05).

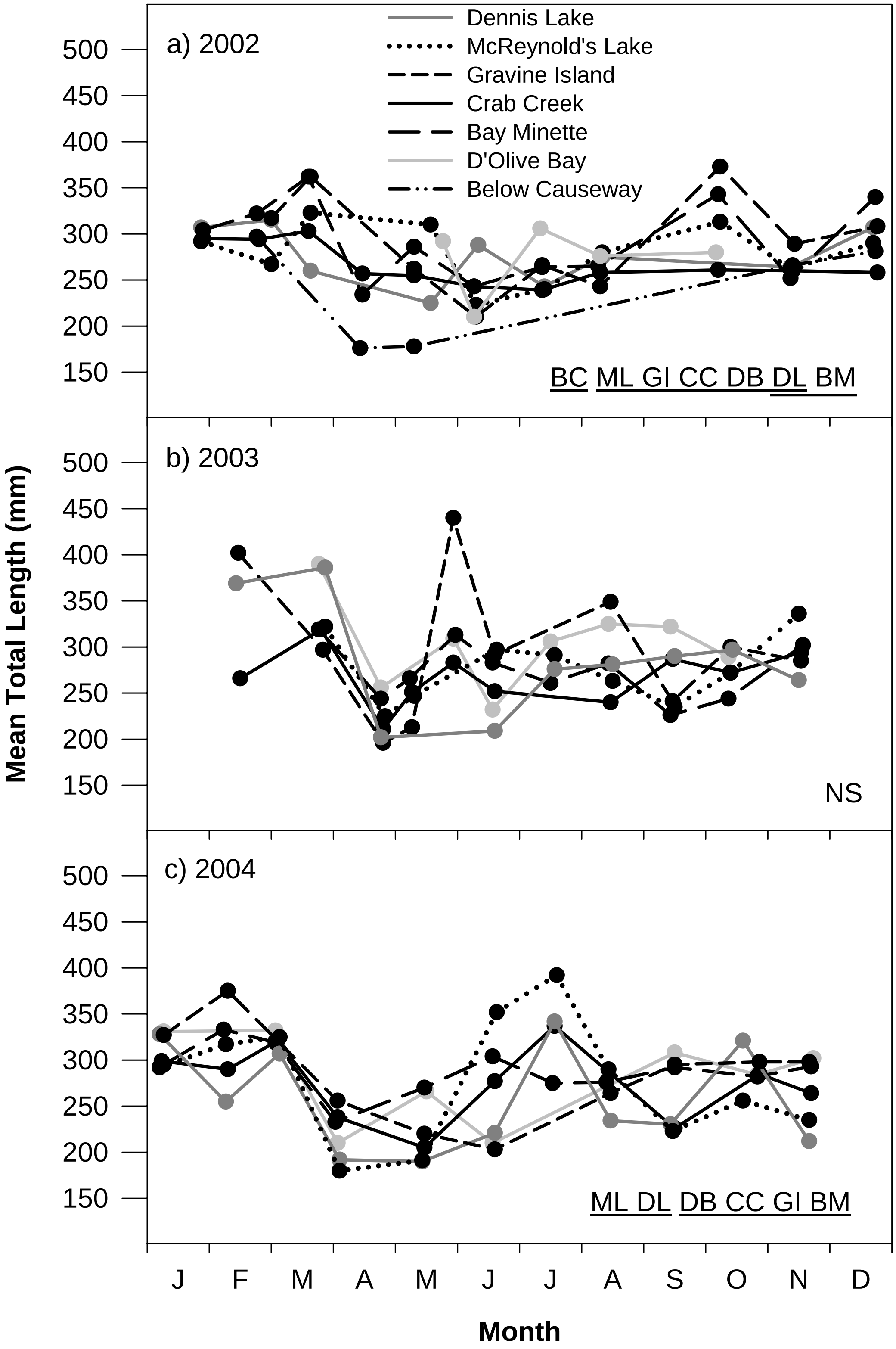
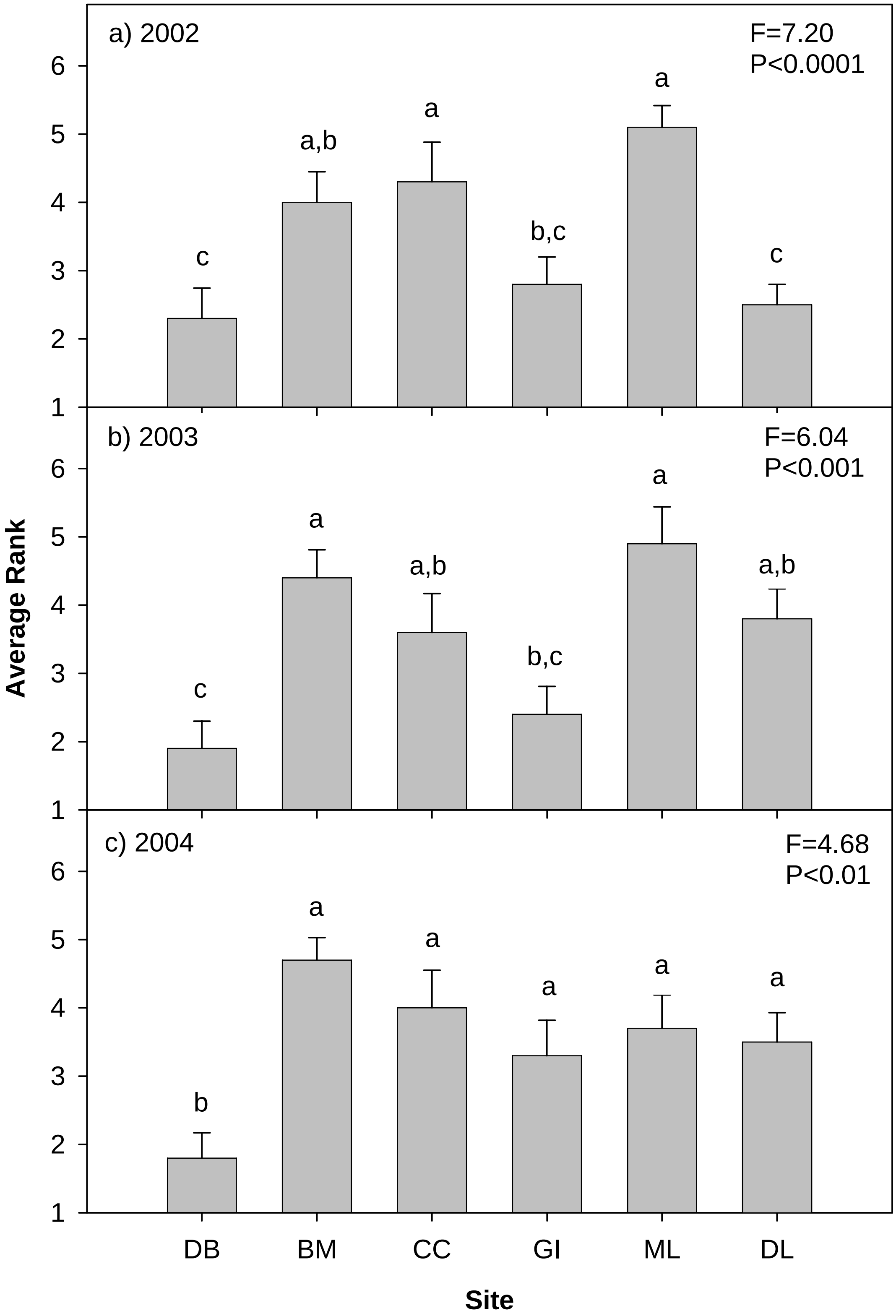

Dennis Lake
McReynold's Lake
Gravine Island
Crab Creek
Bay Minette
D'Olive Bay
Below Causeway
a) 2002
BC ML GI CC DB DL BM
b) 2003
NS
c) 2004
ML DL DB CC GI BM
Mean Total Length (mm)
500
450
400
350
300
250
200
150
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure 6. Average rank for catch rates of largemouth bass during (a) 2002, (b) 2003, and (c) 2004 for all sample sites (D'Olive Bay [DB], Below Causeway [BC], Bay Minette [BM], Crab Creek [CC], Gravine Island [GI], McReynold's Lake [ML], Dennis Lake [DL]) in the Mobile-Tensaw Delta. Data from BC and DB were combined for 2002. Within panels, bars with different letters were significantly different.



a) 2002
F=7.20
P<0.0001
b) 2003
F=6.04
P<0.001
c) 2004
F=4.68
P<0.01
Average Rank
1
2
3
4
5
6
c
a,b
a
b,c
a
c
c
a
a,b
b,c
a
a,b
b
a
a
a
a
a
DB
BM
CC
GI
ML
DL
Site

Figure 7. Monthly mean catch rates (#·hr^{-1}) of largemouth bass by site for (a) 2002, (b) 2003, and (c) 2004 in the Mobile-Tensaw Delta. Site differences are indicated within each graph (two-way ANOVA, Duncan's Multiple Range Comparison, $\alpha = 0.05$).

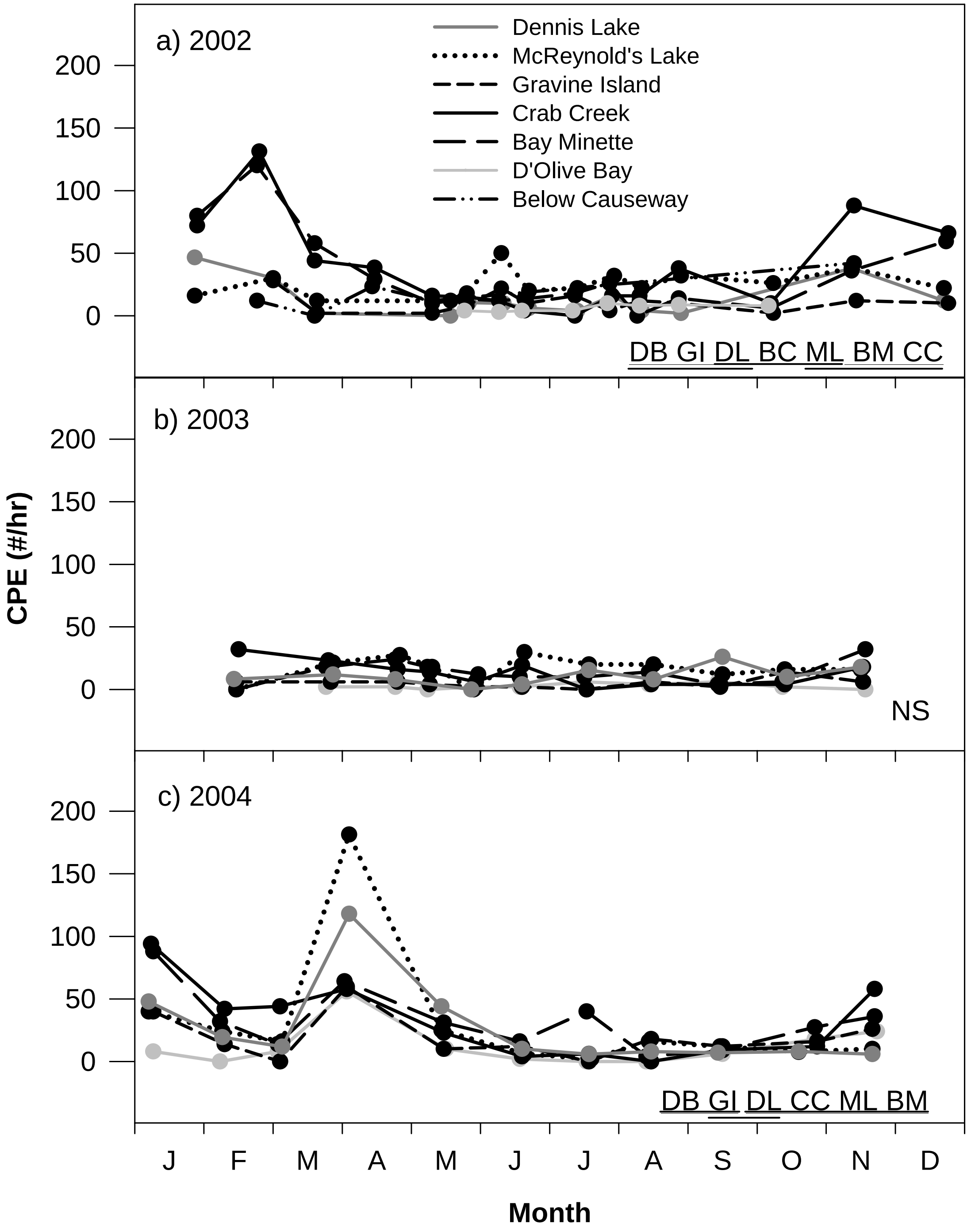
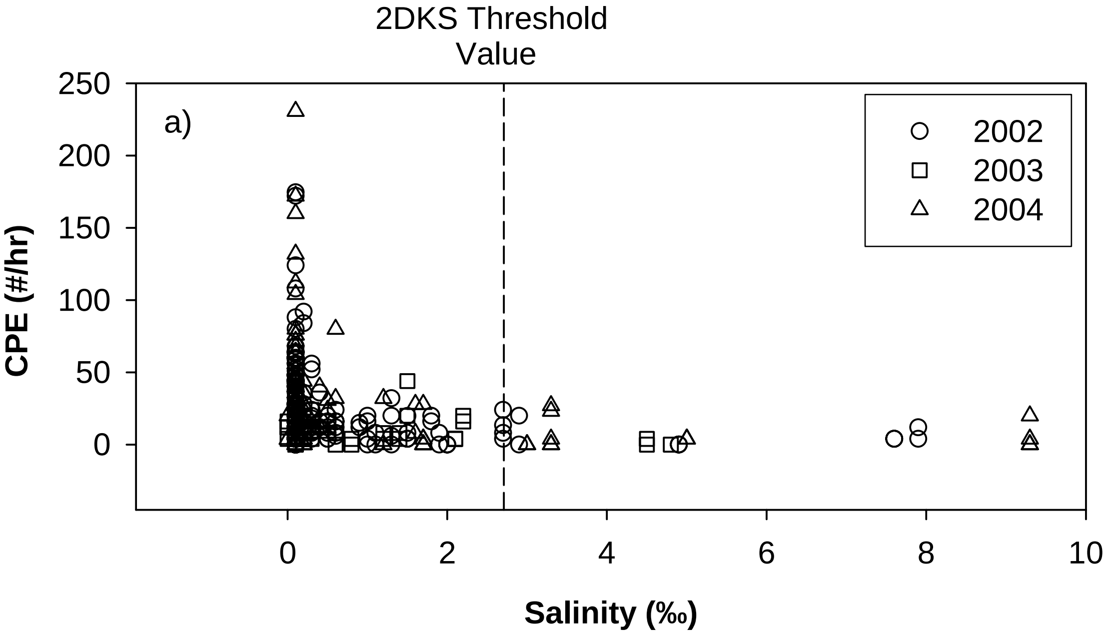

a) 2002
Dennis Lake
McReynold's Lake
Gravine Island
Crab Creek
Bay Minette
D'Olive Bay
Below Causeway
200
150
100
50
0
DB GI DL BC ML BM CC
b) 2003
NS
c) 2004
DB GI DL CC ML BM
CPE (#/hr)
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure 8. (a) Catch rate ($\#\cdot hr^{-1}$) of largemouth bass as a function of salinity at 1 m (‰) for all years (2002-2004) and sample sites. The threshold value for salinity was 2.71‰. (b) Catch rate ($\#\cdot hr^{-1}$) of largemouth bass as a function of temperature at 1 m (°C) for all years (2002-2004) and sample sites. The threshold value for temperature was 16.0°C.


2DKS Threshold
Value
a)
2002
2003
2004
CPE (#/hr)
250
200
150
100
50
0
0
2
4
6
8
10
Salinity (‰)

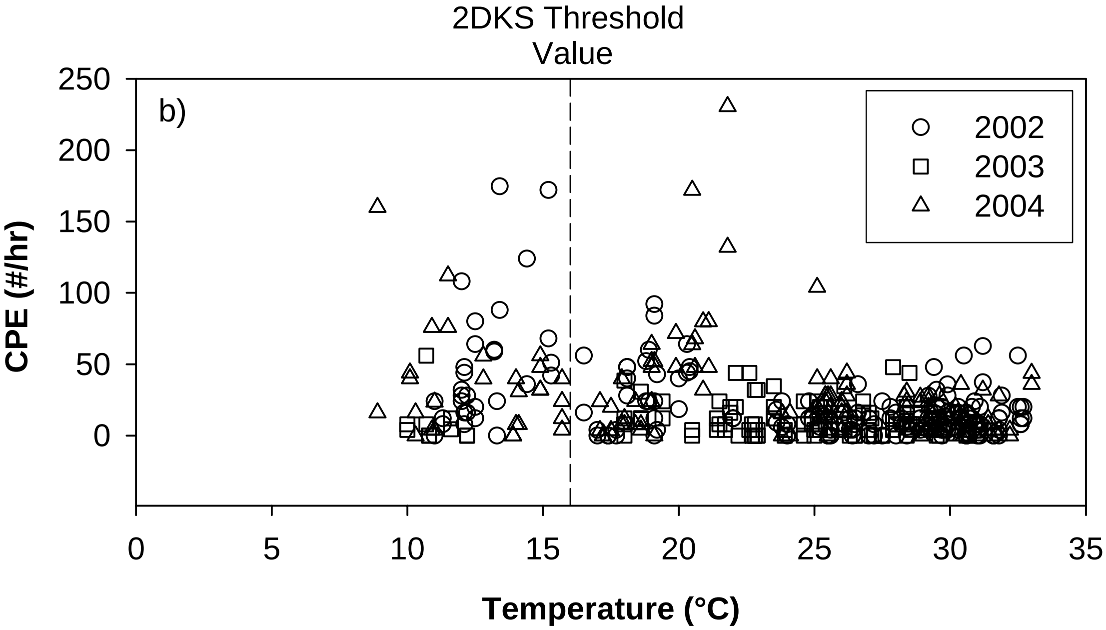

2DKS Threshold
Value
b)
2002
2003
2004
CPE (#/hr)
250
200
150
100
50
0
0
5
10
15
20
25
30
35
Temperature (°C)

Figure 9. Three-dimensional scatter plot of catch rates (#·hr^{-1}) of largemouth bass for all years (2002-2004) and sample sites as a function of both salinity (‰) and temperature (°C) at 1 m depth (a) from the side and (b) from overhead.

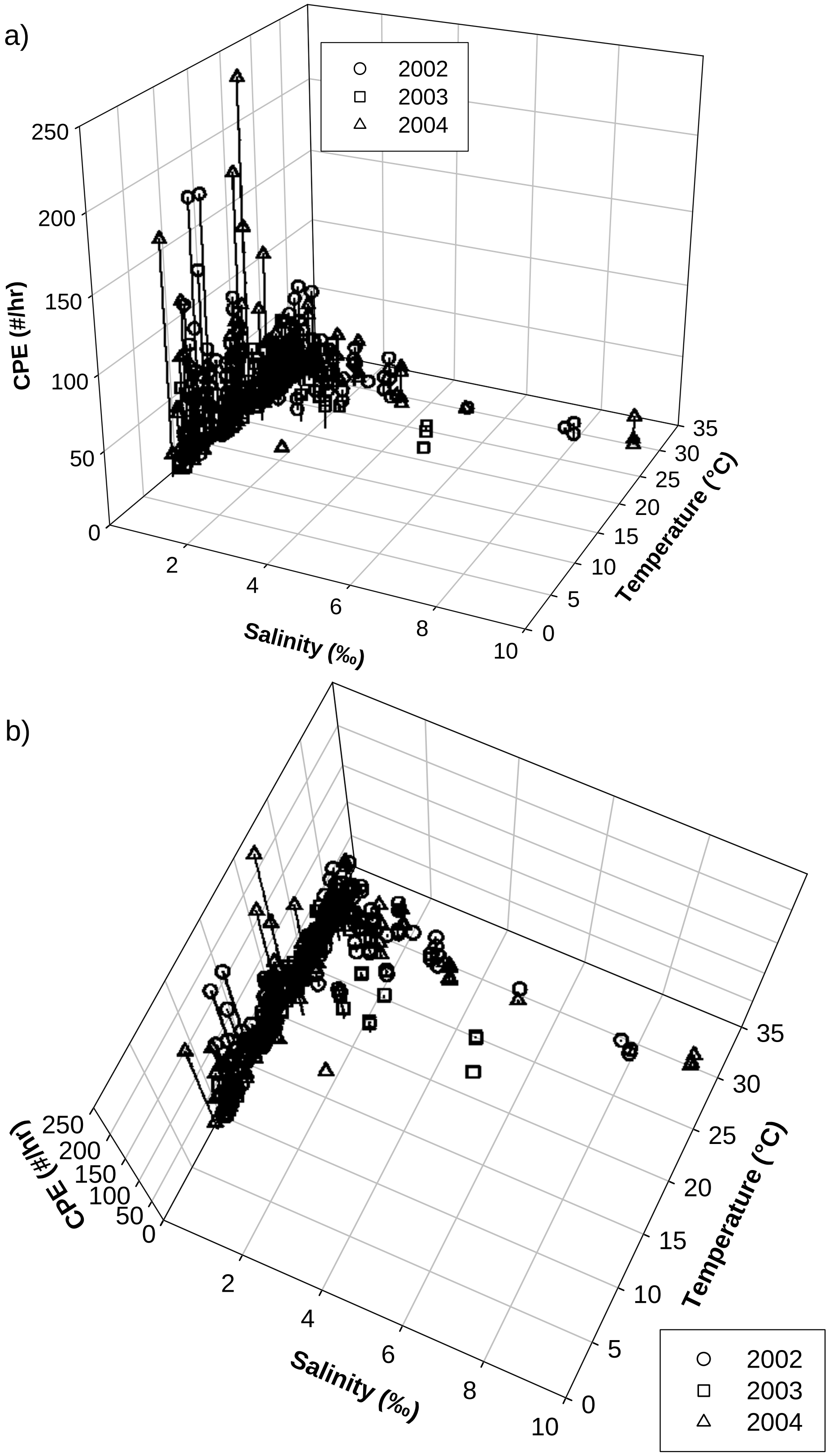

a)
2002
2003
2004
CPE (#/hr)
0
50
100
150
200
250
Salinity (‰)
2
4
6
8
10
Temperature (°C)
0
5
10
15
20
25
30
35
b)
CPE (#/hr)
0
50
100
150
200
250
Salinity (‰)
2
4
6
8
10
Temperature (°C)
0
5
10
15
20
25
30
35
2002
2003
2004

Figure 10. Seasonal patterns in mean per gram diet biomass (g prey·g of bass^{-1}) by downstream and upstream regions during (a,b) 2002, (c,d) 2003, and (e,f) 2004. Within panels, bars with different letters are significantly different and non-significant differences are labeled NS.

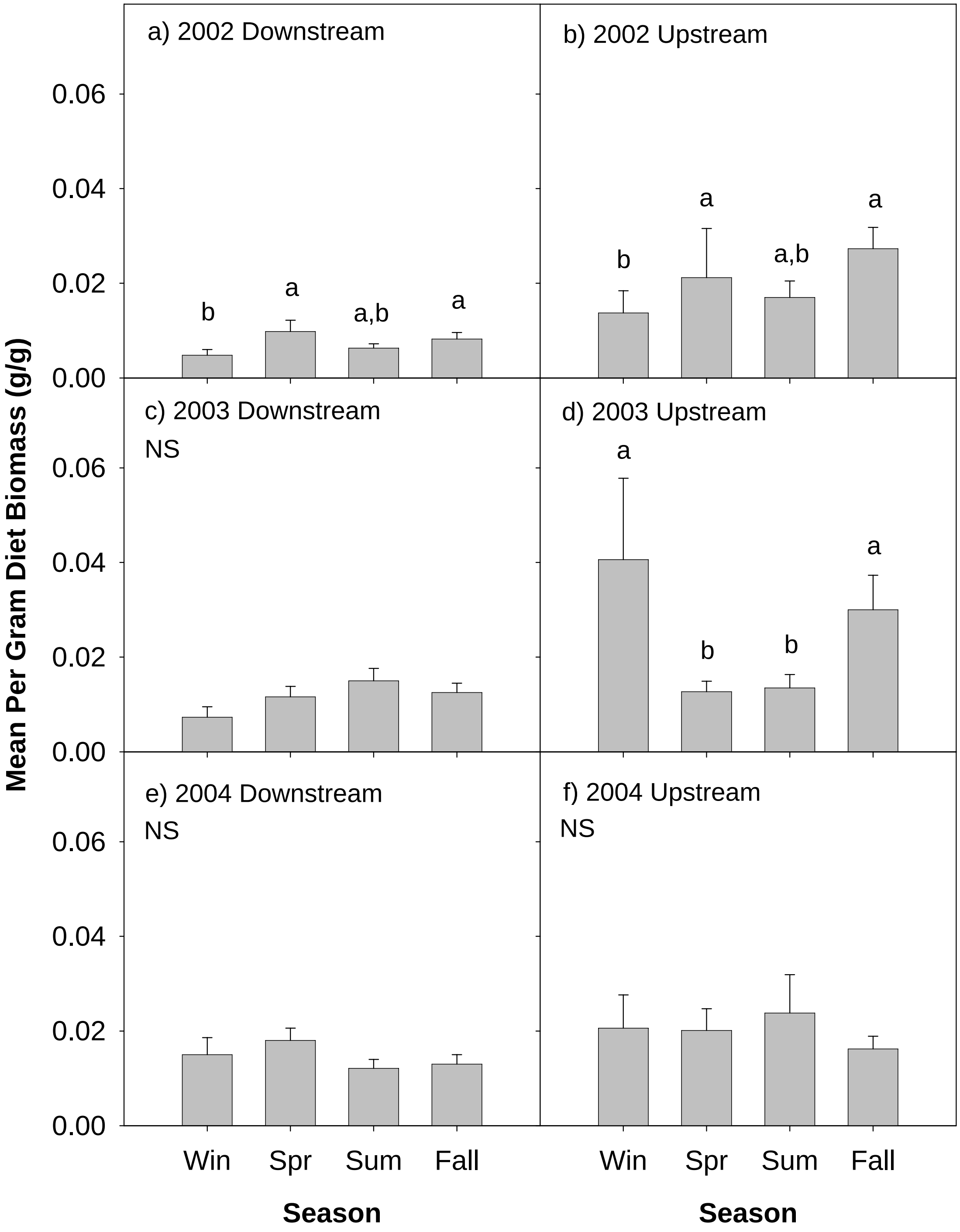

a) 2002 Downstream
b) 2002 Upstream
c) 2003 Downstream
NS
d) 2003 Upstream
e) 2004 Downstream
NS
f) 2004 Upstream
NS
Mean Per Gram Diet Biomass (g/g)
0.00
0.02
0.04
0.06
b
a
a,b
a
b
a
a,b
a
a
b
b
a
Win
Spr
Sum
Fall
Season

Figure 11. Seasonal patterns in percent mean per gram diet biomass (g prey·g of bass^{-1}) of invertebrates and vertebrates by downstream and upstream regions during (a,b) 2002, (c,d) 2003, and (e,f) 2004.

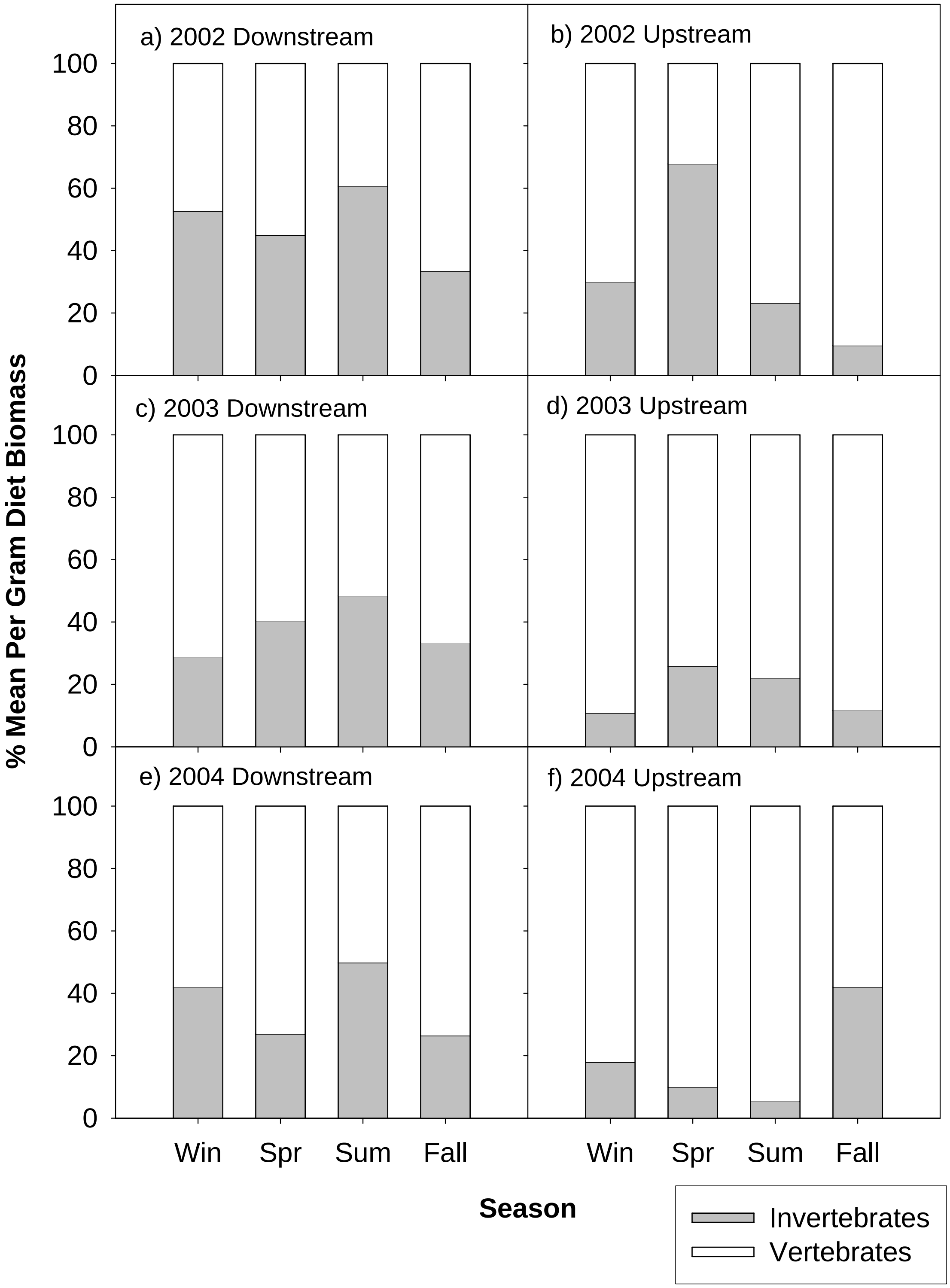

a) 2002 Downstream
b) 2002 Upstream
c) 2003 Downstream
d) 2003 Upstream
e) 2004 Downstream
f) 2004 Upstream
% Mean Per Gram Diet Biomass
0
20
40
60
80
100
Win
Spr
Sum
Fall
Season
Invertebrates
Vertebrates

Figure 12. Seasonal patterns in percent mean per gram diet biomass (g prey·g of bass^{-1}) of freshwater, estuarine, and marine prey by downstream and upstream regions during (a,b) 2002, (c,d) 2003, and (e,f) 2004.

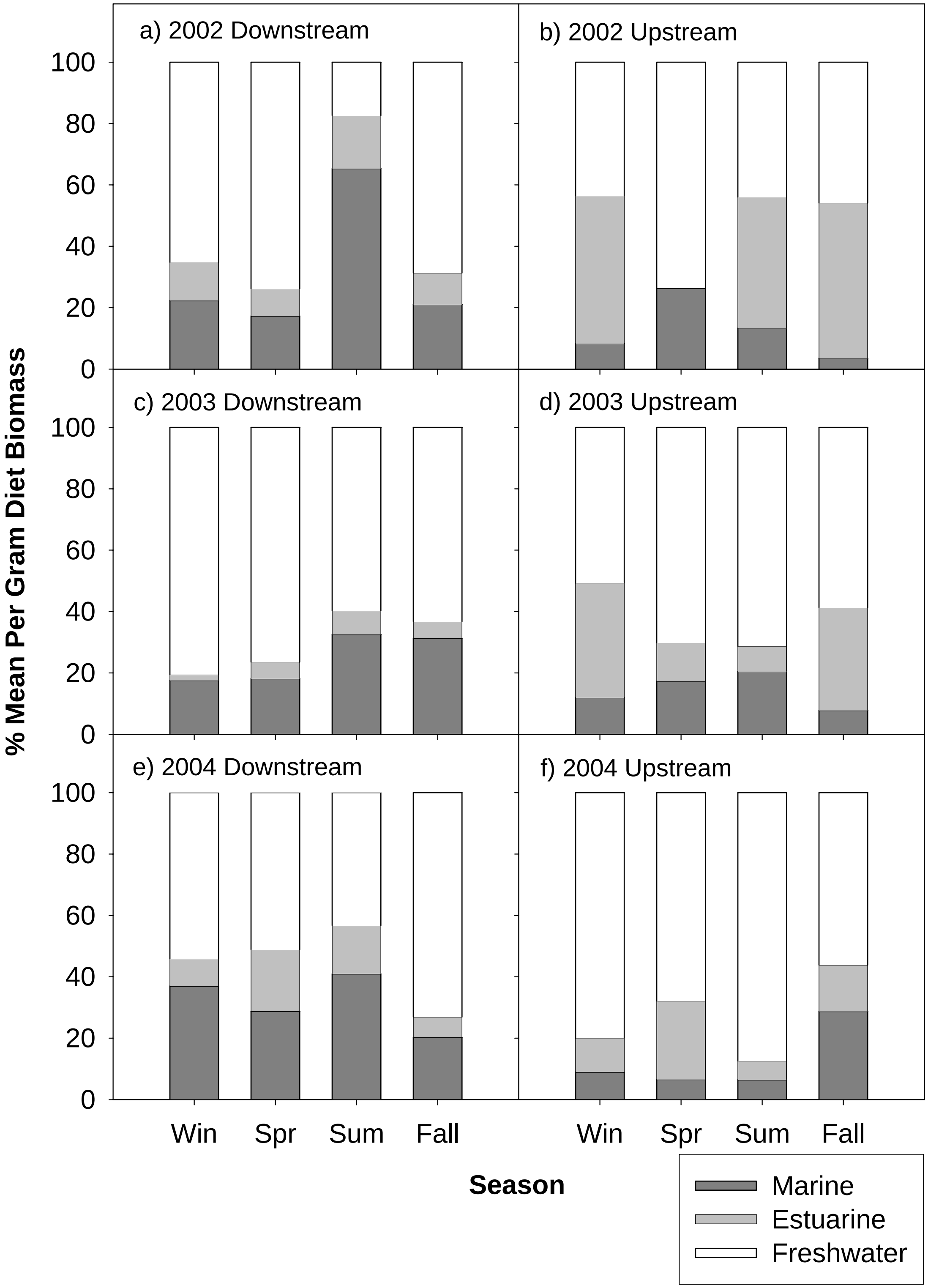

a) 2002 Downstream
b) 2002 Upstream
c) 2003 Downstream
d) 2003 Upstream
e) 2004 Downstream
f) 2004 Upstream
% Mean Per Gram Diet Biomass
0
20
40
60
80
100
Win
Spr
Sum
Fall
Season
Marine
Estuarine
Freshwater

Figure 13. Average rank for relative weight of largemouth bass by size category (small = 150-250 mm; large > 250 mm) across sites for (a,b) 2002, (c,d) 2003, and (e,f) 2004. Within panels, bars with different letters are significantly different.

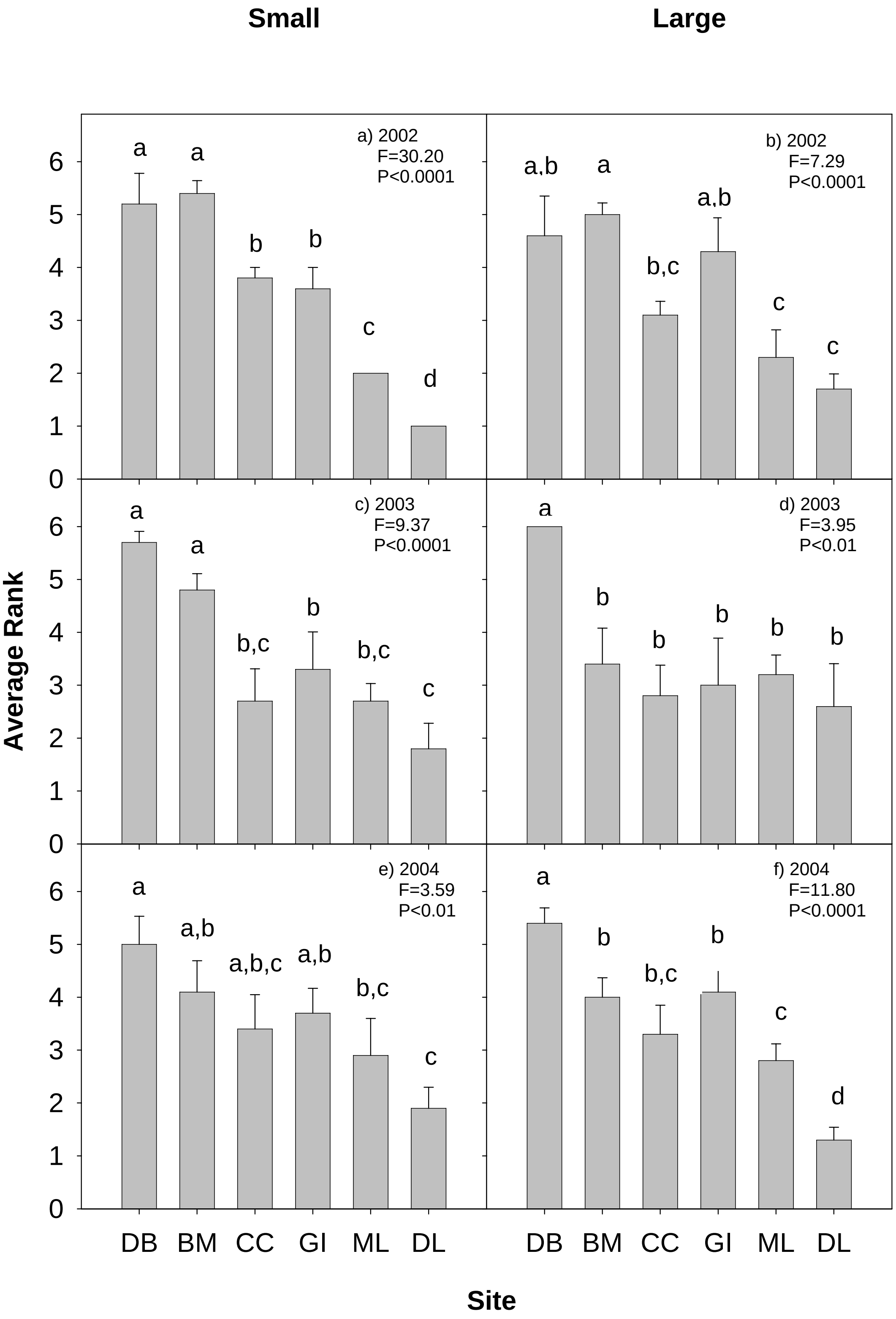

Small
Large
Average Rank
Site
0
1
2
3
4
5
6
a) 2002
F=30.20
P<0.0001
a
a
b
b
c
d
b) 2002
F=7.29
P<0.0001
a,b
a
b,c
a,b
c
c
c) 2003
F=9.37
P<0.0001
a
a
b,c
b
b,c
c
d) 2003
F=3.95
P<0.01
a
b
b
b
b
b
e) 2004
F=3.59
P<0.01
a
a,b
a,b,c
a,b
b,c
c
f) 2004
F=11.80
P<0.0001
a
b
b,c
b
c
d
DB
BM
CC
GI
ML
DL
DB
BM
CC
GI
ML
DL

Figure 14. Age-frequency distributions of fall-collected largemouth bass in both downstream and upstream regions for (a,b) 2002, (c,d) 2003, and (e,f) 2004, where N = total sample size.

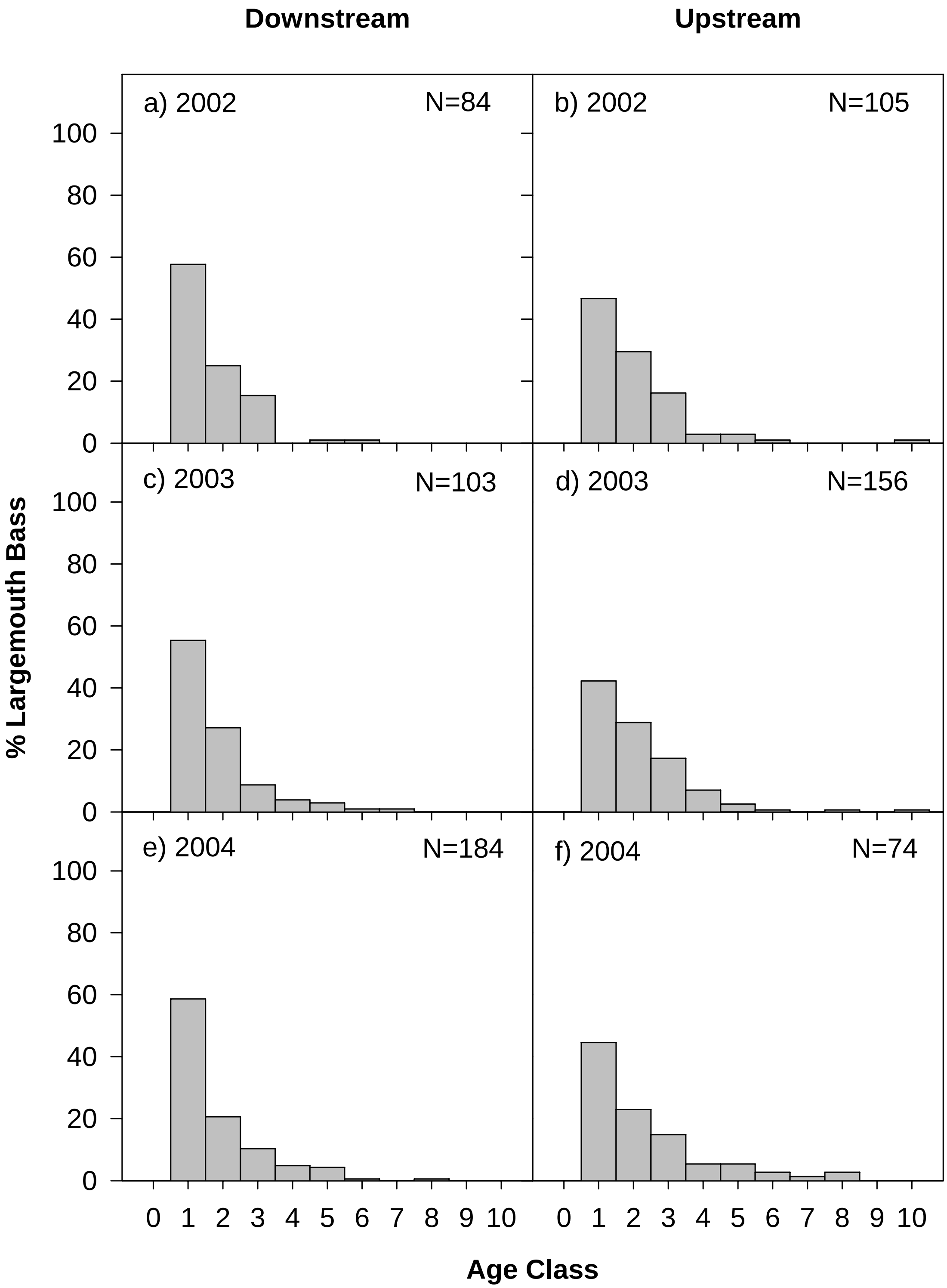

Downstream
Upstream
a) 2002
N=84
b) 2002
N=105
c) 2003
N=103
d) 2003
N=156
e) 2004
N=184
f) 2004
N=74
% Largemouth Bass
0
20
40
60
80
100
0 1 2 3 4 5 6 7 8 9 10
Age Class

Figure 15. Catch-curve regression analysis for fall-collected largemouth bass (age-1 through age-5) from downstream and upstream regions during (a,b) 2002, (c,d) 2003, and (e,f) 2004. Linear regression statistics are included on each panel. Note that the y-axis is log scale.

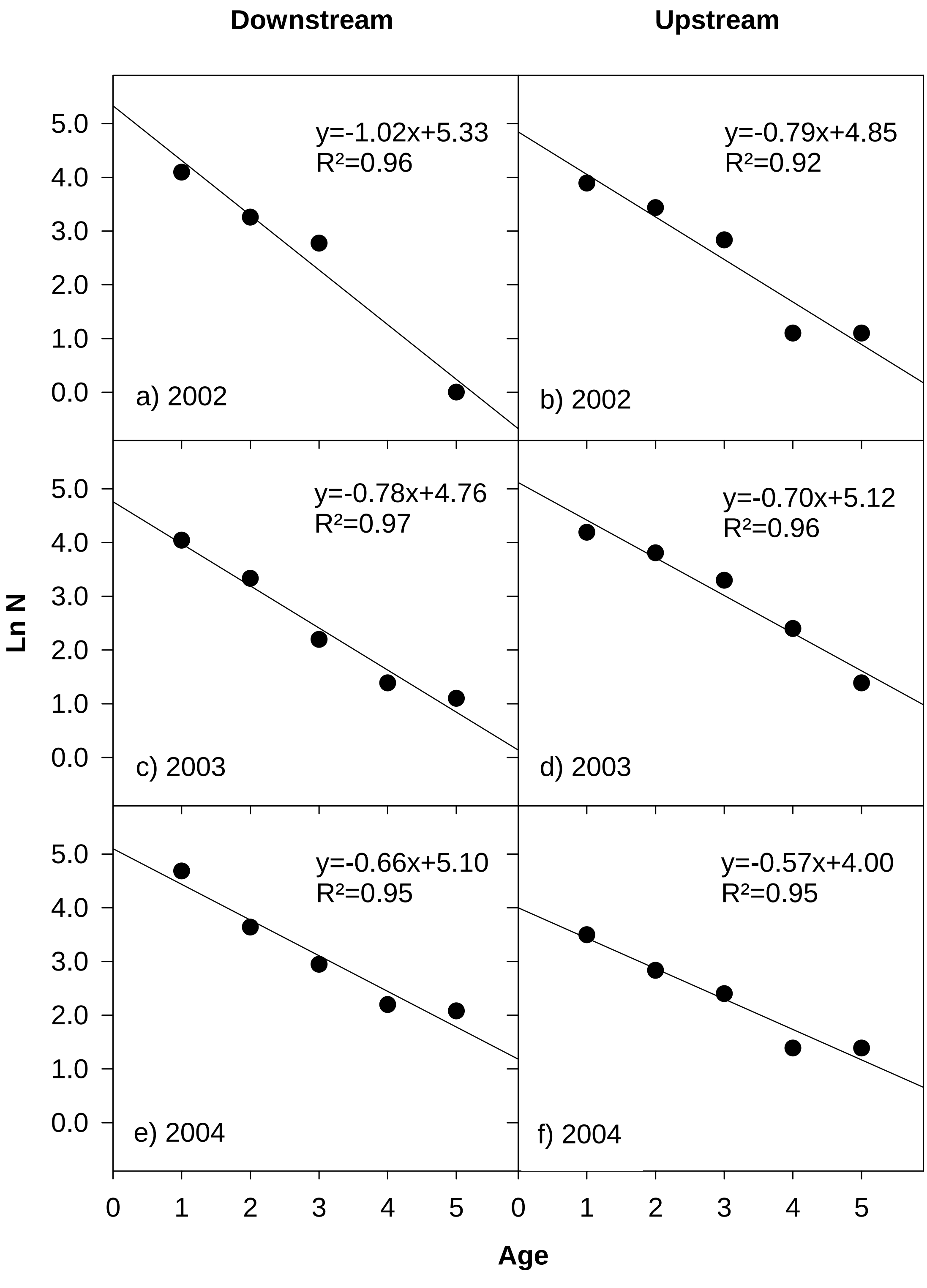

Downstream
Upstream
Ln N
5.0
4.0
3.0
2.0
1.0
0.0
y=-1.02x+5.33
R²=0.96
a) 2002
y=-0.79x+4.85
R²=0.92
b) 2002
y=-0.78x+4.76
R²=0.97
c) 2003
y=-0.70x+5.12
R²=0.96
d) 2003
y=-0.66x+5.10
R²=0.95
e) 2004
y=-0.57x+4.00
R²=0.95
f) 2004
0
1
2
3
4
5
Age

Figure 16. (a) Age-frequency distribution of largemouth bass collected in fall 2004 from Monroe County Lake. (b) Catch-curve regression analysis for largemouth bass (age-1 through age-3) collected in fall 2004 from Monroe County Lake. Regression statistics are included in this panel. Note that the y-axis is log scale.

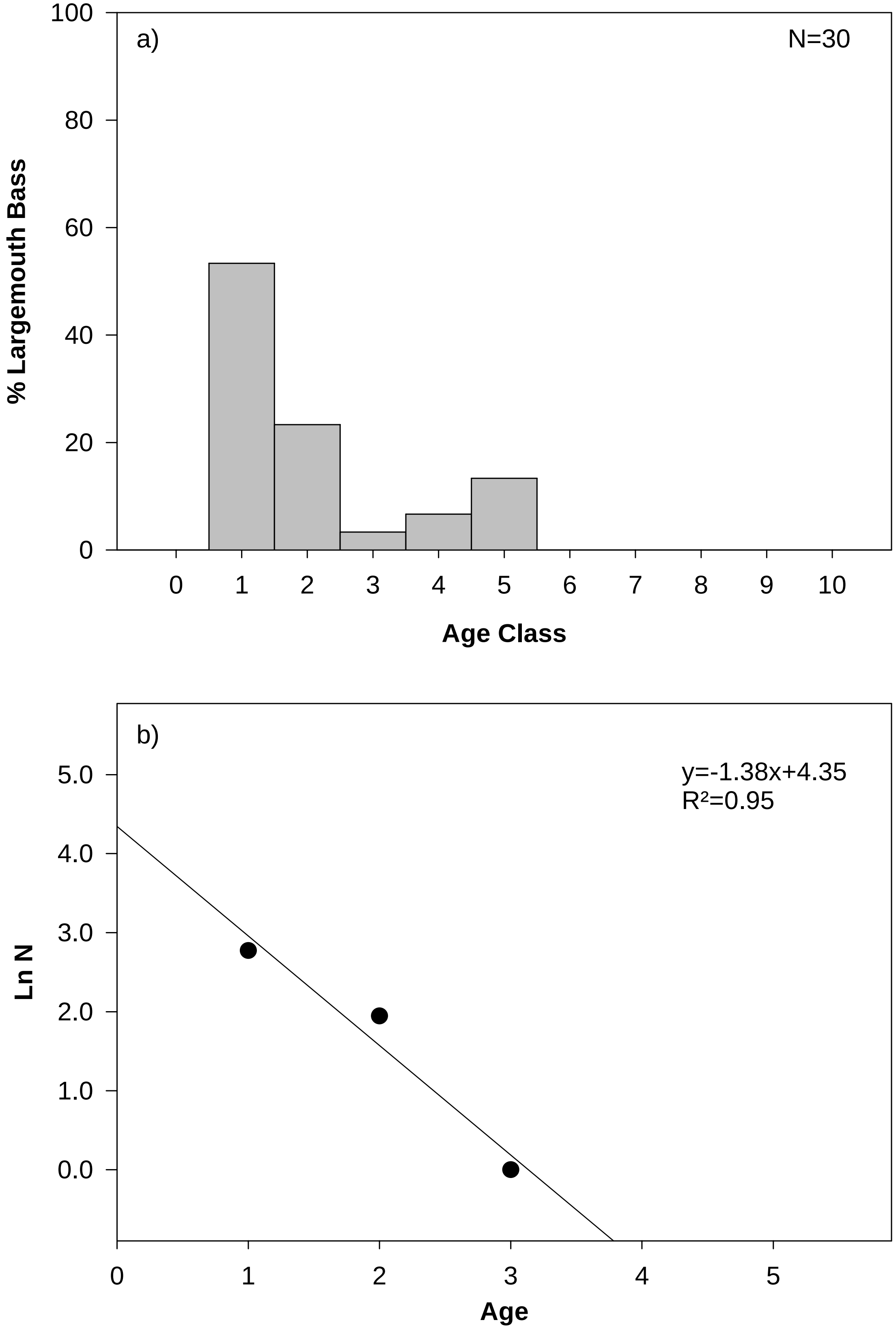
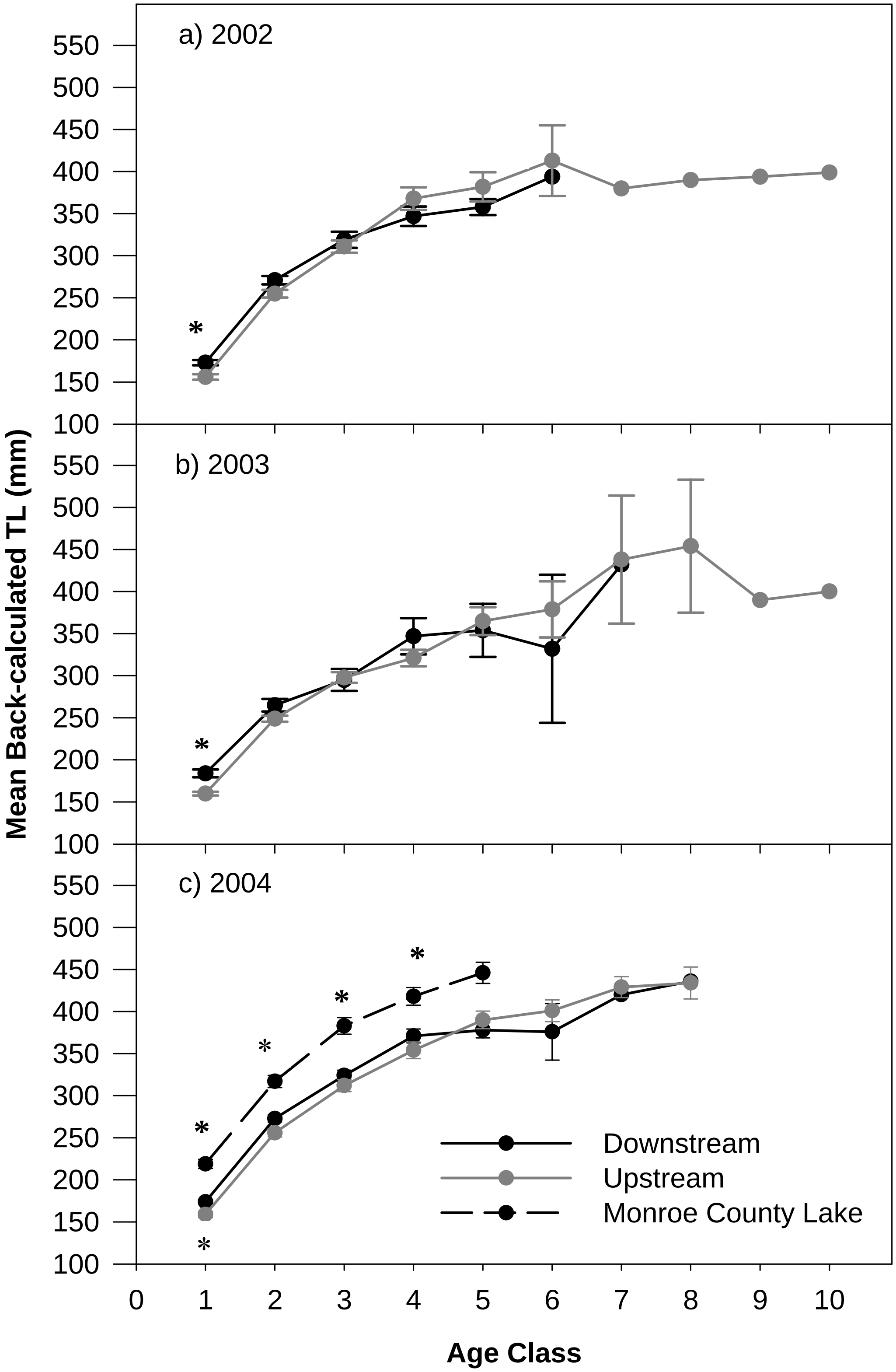

a)
N=30
% Largemouth Bass
0
20
40
60
80
100
0
1
2
3
4
5
6
7
8
9
10
Age Class
b)
y=-1.38x+4.35
R²=0.95
Ln N
0.0
1.0
2.0
3.0
4.0
5.0
0
1
2
3
4
5
Age

Figure 17. Growth curves of fall-collected largemouth bass in downstream and upstream regions for (a) 2002, (b) 2003, and (c) 2004. Also included in (c) is the growth curve for fall-collected largemouth bass from Monroe County Lake. Significant differences are indicated by an asterisk.



a) 2002
b) 2003
c) 2004
Mean Back-calculated TL (mm)
100
150
200
250
300
350
400
450
500
550
Age Class
0
1
2
3
4
5
6
7
8
9
10
*
Downstream
Upstream
Monroe County Lake

Figure 18. (a) Map of the Mobile Delta with locations of monthly sample sites (D'Olive Bay, Bay Minette Bay, Crab Creek, Gravine Island, McReynold's Lake, and Dennis Lake). (b) Map of the upstream tournament release site (Live Oak Landing) on the Tensaw River 4.8 river-km upstream of I-65. (c) Map of Dennis Lake, upstream acoustic telemetry site. (d) Map of Bay Minette, dowstream acoustic telemetry site. (e) Map of the area surrounding the downstream tournament release site (USS Alabama). All release sites are denoted by a ✦.

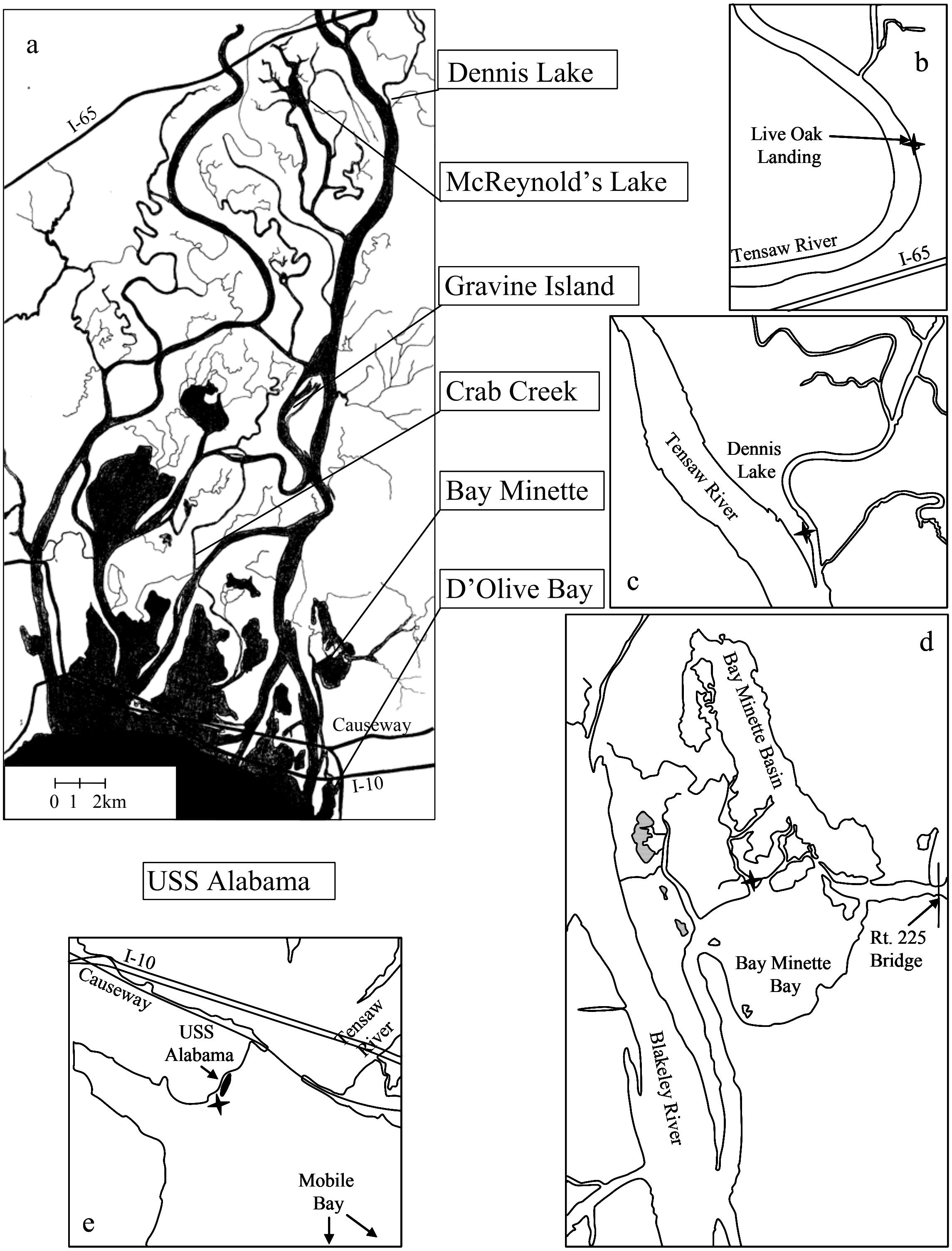
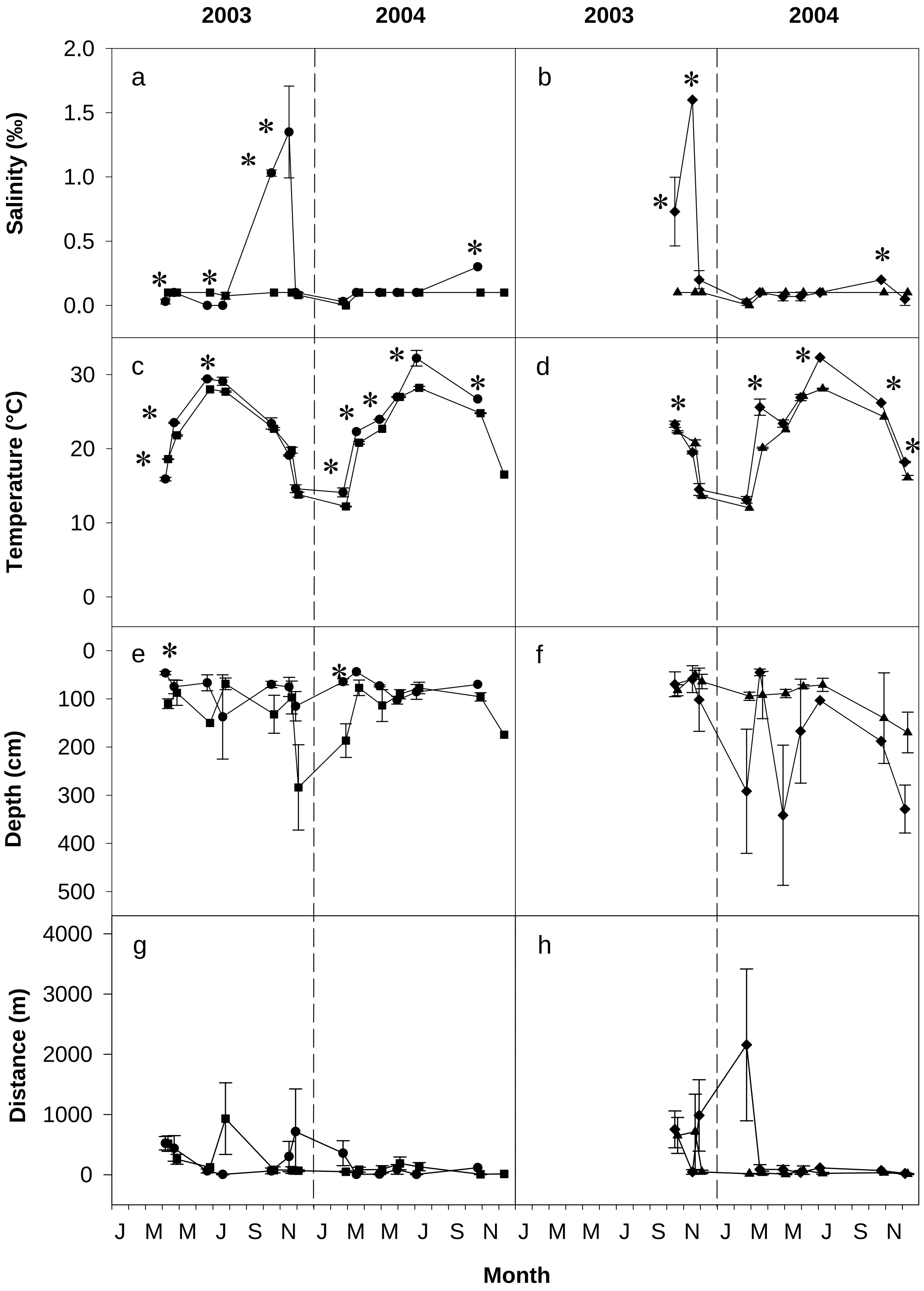

a
I-65
Dennis Lake
McReynold's Lake
Gravine Island
Crab Creek
Bay Minette
D'Olive Bay
Causeway
I-10
0 1 2km
USS Alabama
b
Live Oak
Landing
Tensaw River
I-65
c
Tensaw River
Dennis
Lake
d
Bay Minette Basin
Rt. 225
Bridge
Bay Minette
Bay
Blakeley River
e
I-10
Causeway
Tensaw
River
USS
Alabama
Mobile
Bay

Figure 19. Mean salinity (a), mean surface water temperature (c), mean total depth (e), and mean total distance (g) for relocations of acoustically tagged bass from spring release in Bay Minette Bay (●) and Dennis Lake (■). Mean salinity (b), mean surface water temperature (d), mean total depth (f), and mean total distance (h) for relocations of acoustically tagged bass from fall release in Bay Minette Bay (♦) and Dennis Lake (▲). Significant differences ($P < 0.05$) are indicated by a *.


2003
2004
2003
2004
a
b
c
d
e
f
g
h
Salinity (‰)
Temperature (°C)
Depth (cm)
Distance (m)
2.0
1.5
1.0
0.5
0.0
30
20
10
0
0
100
200
300
400
500
4000
3000
2000
1000
0
J M M J S N J M M J S N J M M J S N J M M J S N
Month
*

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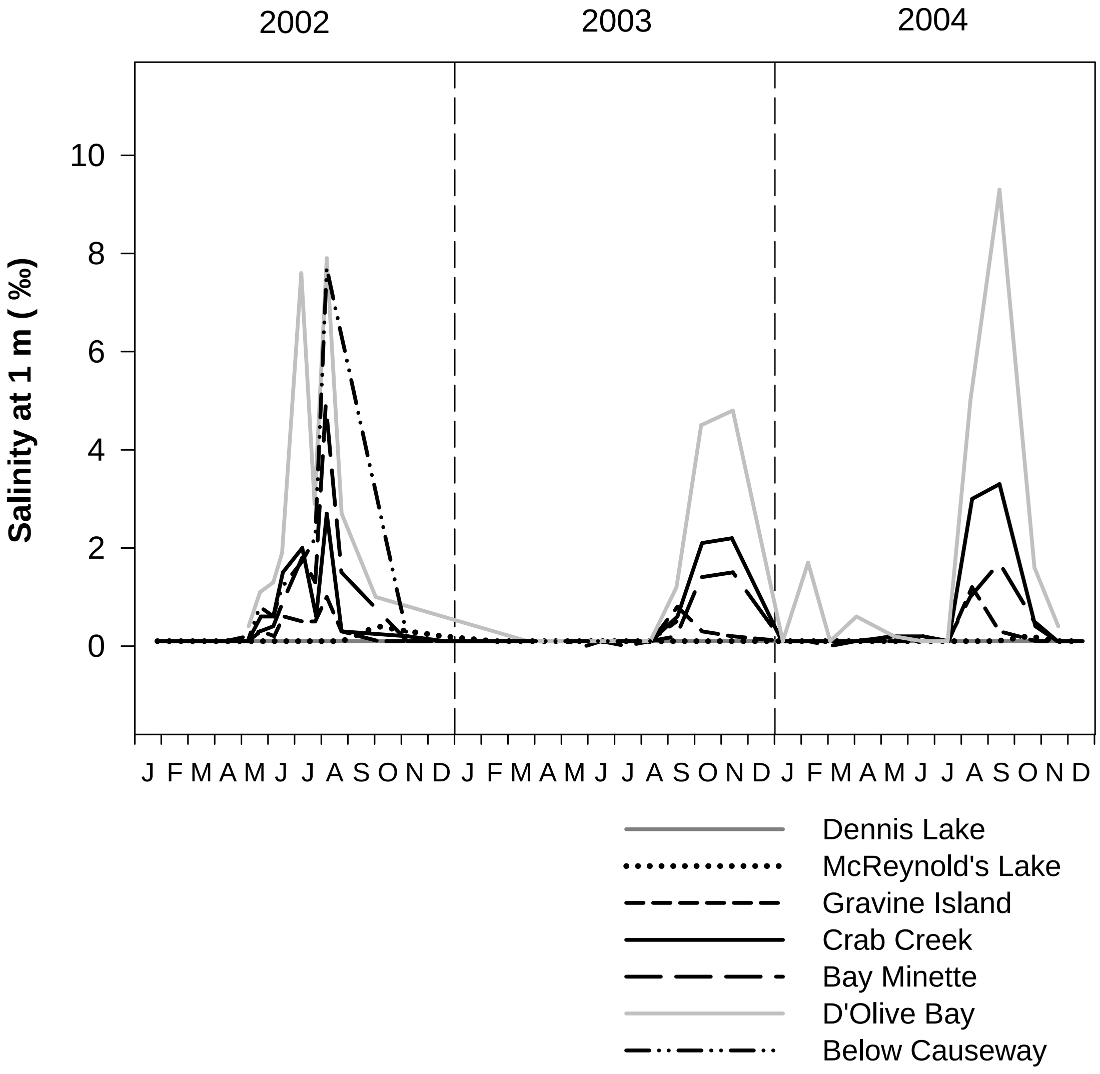
APPENDICES

Appendix A. Monthly salinity values (‰) at 1-m depth for seven sample sites during 2002-2004 in the Mobile-Tensaw Delta.


2002
2003
2004
Salinity at 1 m (‰)
10
8
6
4
2
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
Dennis Lake
McReynold's Lake
Gravine Island
Crab Creek
Bay Minette
D'Olive Bay
Below Causeway

Appendix B. Description of hurricane activity in or nearby Mobile-Tensaw Delta (2002-2004).

According to the National Weather Service (NWS; www.nhc.noaa.gov), hurricane and tropical storm activity was greater in the vicinity of the Mobile-Tensaw Delta during 2002 and 2004 than 2003. In 2002, Hurricane Isadore (26 September) made landfall as a tropical storm near Grand Isle, LA and rainfall totals in the lower Mobile-Tensaw Delta and Mobile Bay were 20.3-27.9 cm. Precipitation effects were weaker (< 5.1 cm) from Tropical Storm Hanna (14 September 2002), making landfall along the Alabama-Mississippi border, and Hurricane Lili (3 October 2002), making landfall in Intracoastal City, Louisiana. Highest sustained winds (56-119 $km \cdot h^{-1}$) and peak wind gusts (93-193 $km \cdot h^{-1}$) during or after landfall were reported for all of the 2002 storms. In 2003, Tropical Storm Bill (30 June 2003) made landfall along the Louisiana coast and was the storm with a landfall closest to our study area in 2003, but storm effects were not reported by the NWS for Alabama and were likely minimal in the Mobile-Tensaw Delta. The most direct landfall (east of Gulf Shores, AL; 15 September 2004) was from Hurricane Ivan, which moved inland along the eastern portion of Mobile Bay and the eastern edge of the Mobile-Tensaw Delta, creating extensive damage along the coast as well as inland. Highest precipitation amounts in our study area (from Spanish Fort, AL to Mobile, AL) were about 20.3 cm. Complete records of peak winds were not available in our study area, possibly due to storm damage, but records east of the eyewall (near Pensacola, FL) at landfall indicated highest sustained winds of 141 $km \cdot h^{-1}$ and wind gusts of 172 $km \cdot h^{-1}$.

Due to Hurrricane Ivan, a reported 2.7 million acres of damaged timber occurred throughout woodlands and forests in Alabama (Alabama Forestry Commission; www.forestry.state.al.us). In the forested upstream sites of the Mobile-Tensaw Delta, fallen trees were abundant along shorelines, and the defoliated and bark-stripped trees that remained sprouted new foliage by November 2004 (personal observation). The resulting organic material may have been introduced into the nearby aquatic habitat, causing large scale decomposition of vegetation and subsequent low dissolved oxygen levels possibly responsible for widespread fish kills reported throughout upstream backwaters (David L. Armstrong, Jr.; Alabama Division of Fish and Wildlife; personal communication).

Appendix C. Temporal variation in mean size among-years (2002-2004).

Despite variability in the magnitude and timing of the salinity peak among years, mean length of adult largemouth bass did not differ significantly among years for any site (Fig. 5; two-way ANOVA; year effect; all sites $P > 0.27$). Differences among months were significant for all sites (two-way ANOVA; month effect; all $P < 0.0001$). A significant interaction effect (two-way ANOVA, year*month effect) occurred at Bay Minette Bay, Crab Creek, and McReynold's Lake (all $P < 0.01$), while an interaction effect was marginally significant at Gravine Island ($F = 1.74$, $P < 0.055$).

Appendix D. Prey consumption patterns for all prey types among-years, invertebrates v. vertebrates among-years, and prey origin within regions and among-years (2002-2004).

All prey types among-years

Prey consumption patterns were not similar among years either upstream or downstream. While the overall model (two-way ANOVA) was not significant upstream ($F = 1.91$, $P = 0.21$), year differences (two-way ANOVA; year effect; Fig. 10) were significant downstream ($F = 8.21$, $P < 0.001$). Prey consumption downstream was significantly greater (Duncan's Multiple Range Test; $P < 0.05$) in 2004 (mean = 0.0154 $g{\cdot}g^{-1}$) and 2003 (mean = 0.0122 $g{\cdot}g^{-1}$) than 2002 (mean = 0.0074 $g{\cdot}g^{-1}$).

Invertebrates vs. vertebrates among-year variation.

Among-year differences in invertebrates were not present downstream or upstream. Although year ($F = 0.30$, $P = 0.74$) and season ($F = 0.69$, $P = 0.56$) did not differ significantly (two-way ANOVA; year effect; Fig. 11) upstream, a significant interaction (two-way ANOVA; year*season effect) was found ($F = 3.69$, $P < 0.01$). While the overall model (one-way ANOVA) was not significant in 2003 ($F = 0.31$, $P = 0.82$), seasonal variation was significant (one-way ANOVA; season effect) in both 2002 ($F = 2.75$, $P = 0.04$) and 2004 ($F = 6.22$, $P < 0.001$). (See invertebrate vs. vertebrate within-year variation for details on interaction effects). The overall model (two-way ANOVA) was not significant downstream ($F = 1.55$, $P = 0.12$). For vertebrates (Fig. 18), among-year differences were significant (two-way ANOVA; year effect) downstream ($F = 6.76$, $P < 0.01$) with significantly greater consumption in 2004 (mean = 0.0238 $g{\cdot}g^{-1}$) and 2003 (mean = 0.0159 $g{\cdot}g^{-1}$) than 2002 (mean = 0.0082 $g{\cdot}g^{-1}$). The overall model (two-way ANOVA) was not significant upstream ($F = 1.59$, $P = 0.11$).

Prey origin within regions.

Differences in prey biomass based on origin (e.g., freshwater, estuarine, or marine) were highly significant (one-way ANOVA; prey effect; Fig. 12) downstream and upstream in all years (all $P < 0.0001$). Significantly more (Duncan's Multiple Range Test; $P < 0.05$) freshwater prey was consumed downstream (2002 = 0.0186 $g \cdot g^{-1}$, 2003 = 0.0284 $g \cdot g^{-1}$, 2004 = 0.0258 $g \cdot g^{-1}$) and upstream (2002 = 0.0269 $g \cdot g^{-1}$, 2003 = 0.0325 $g \cdot g^{-1}$, 2004 = 0.0368 $g \cdot g^{-1}$) in all years. Downstream in all years, significantly more (Duncan's Multiple Range Test; $P<0.05$) marine prey (2002 = 0.0070 $g \cdot g^{-1}$, 2003 = 0.0104 $g \cdot g^{-1}$, 2004 = 0.0130 $g \cdot g^{-1}$) was consumed than estuarine prey (2002 = 0.0027 $g \cdot g^{-1}$, 2003 = 0.0025 $g \cdot g^{-1}$, 2004 = 0.0073 $g \cdot g^{-1}$). Upstream in 2002, estuarine prey (mean = 0.0321 $g \cdot g^{-1}$) did not differ (Duncan's Multiple Range Test; $P < 0.05$) from freshwater prey, and marine prey (mean = 0.0056 $g \cdot g^{-1}$) was significantly less than other prey types. No differences among upstream prey types were found in 2003 or 2004.

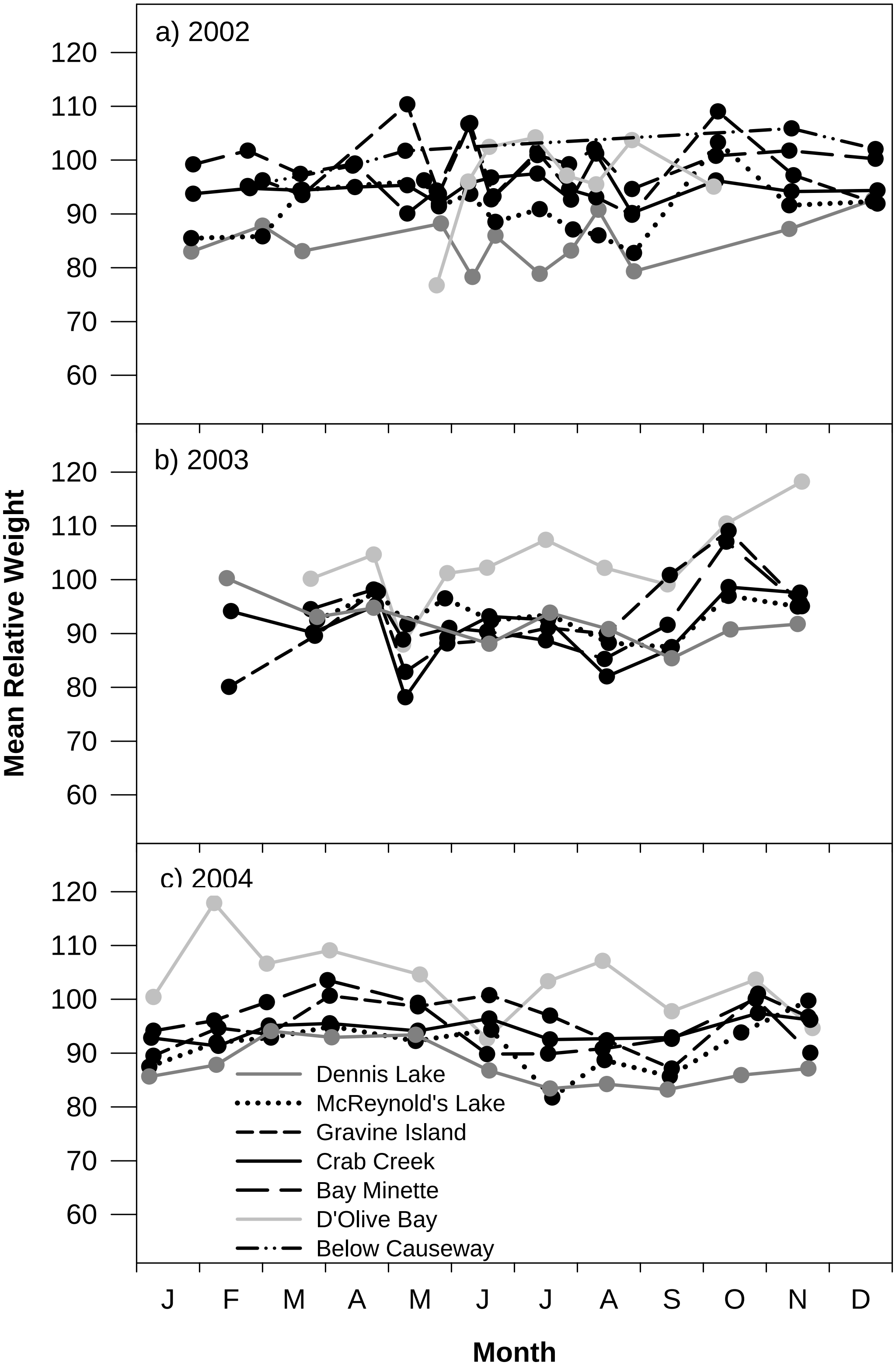
Prey origin among-year variation.

A common among-year pattern in estuarine and marine prey occurred downstream but not upstream (Fig. 12). Overall models (two-way ANOVA) were not significant for freshwater prey (all $P > 0.44$). Estuarine prey differed significantly (two-way ANOVA; year effect) among years downstream ($F = 4.12$, $P < 0.05$) and upstream ($F = 15.86$, $P < 0.0001$). However, downstream estuarine prey was significantly greater (Duncan's Multiple Range Test; $P < 0.05$) in 2004 (mean = 0.0073 $g \cdot g^{-1}$) than 2002 (mean = 0.0027 $g \cdot g^{-1}$), and 2003 (mean = 0.0026 $g \cdot g^{-1}$) was not different from other years; while upstream estuarine prey was significantly greater (Duncan's Multiple Range

Test; $P < 0.05$) in 2002 (mean = 0.0321 $g{\cdot}g^{-1}$) than 2003 (mean = 0.0047 $g{\cdot}g^{-1}$) and 2004 (mean = 0.0090 $g{\cdot}g^{-1}$).

Marine prey also differed significantly (two-way ANOVA; year effect; Fig. 12) among-years downstream ($F = 4.97$, $P < 0.01$) and upstream ($F = 3.35$, $P < 0.05$). Similar to downstream estuarine prey, downstream marine prey was significantly higher (Duncan's Multiple Range Test; $P < 0.05$) during 2004 (mean = 0.0130 $g{\cdot}g^{-1}$) than 2002 (mean = 0.0070 $g{\cdot}g^{-1}$), and 2003 (mean = 0.0103 $g{\cdot}g^{-1}$) did not differ from other years. Unlike upstream estuarine prey, upstream marine prey was significantly higher (Duncan's Multiple Range Test; $P < 0.05$) during 2003 (mean = 0.0125 $g{\cdot}g^{-1}$) than 2002 (mean = 0.0056 $g{\cdot}g^{-1}$) and 2004 (mean = 0.0056 $g{\cdot}g^{-1}$). Although season ($F = 1.18$, $P = 0.32$) was not significant (two-way ANOVA; season effect), a significant interaction (two-way ANOVA; year*season effect; $F = 2.70$, $P < 0.5$) occurred, and season was significant in all years (all $P < 0.05$). (See prey-origin within-year variation for details on interaction effects).

Appendix E. Monthly mean relative weight (Wr) of largemouth bass by site for (a) 2002, (b) 2003, and (c) 2004.


a) 2002
b) 2003
c) 2004
120
110
100
90
80
70
60
Mean Relative Weight
Dennis Lake
McReynold's Lake
Gravine Island
Crab Creek
Bay Minette
D'Olive Bay
Below Causeway
J
F
M
A
M
J
J
A
S
O
N
D
Month

Appendix F. Relative weight patterns among-sites, among-years, and within years (2002-2004).

Differences in mean monthly relative weight (Wr) among sites (two-way ANOVA; site effect; Appendix 6) were significant across years (all $P < 0.0001$), and mean Wr generally decreased from downstream to upstream among sites. Although monthly variability was significant (two-way ANOVA; month effect) in all years (all $P < 0.01$), a significant interaction (two-way ANOVA; site*month effect) occurred only during 2002 ($F = 1.54$, $P < 0.05$) and 2004 ($F = 1.86$, $P < 0.001$). (See temporal variation within-years section for more details concerning interaction effects.)

Among-year mean Wr was more stable at mid-gradient sites as opposed to sites occupying end positions along the downstream-upstream gradient. Mean Wr differed significantly among years (two-way ANOVA; year effect; Appendix 6) at D'Olive Bay, Bay Minette Bay, and Dennis Lake (all $P < 0.01$). Significantly higher mean Wr (Duncan's Multiple Range Test; $P < 0.05$) occurred in 2003 at Dennis Lake (Wr = 91.6), in 2002 at Bay Minette Bay (Wr = 99.98), and both 2003 (Wr = 104.6) and 2004 (Wr = 103.1) at D'Olive Bay; while significantly lower Wr (Duncan's Multiple Range Test; $P < 0.05$) occurred at D'Olive Bay (Wr = 96.3) and Dennis Lake (Wr = 85.2) in 2002 and Bay Minette Bay during both 2003 (Wr = 95.2) and 2004 (Wr = 96.4). No among-year differences were found at Crab Creek, Gravine Island, or McReynold's Lake (all $P \geq 0.09$). Monthly variability was significant (two-way ANOVA; month effect) for all sites (all $P < 0.01$) except Crab Creek ($F = 1.66$, $P = 0.08$), and a significant interaction (two-way ANOVA; year*month effect) was found for D'Olive Bay ($F = 2.85$, $P < 0.01$) and Bay Minette Bay ($F = 2.93$, $P < 0.0001$).

Mean Wr tended to be greater during fall months during 2002 and 2003 and greater during both spring and fall in 2004. Significant monthly variation (one-way

ANOVA; month effect; Appendix 6) in 2002 mean Wr occurred only at McReynold's Lake ($F = 6.10$, $P < 0.0001$), where mean Wr was significantly greater (Duncan's Multiple Range Test; $P < 0.05$) during October (mean Wr = 103.3). In 2003, significant monthly variation (one-way ANOVA; month effect) in mean Wr occurred only at Bay Minette Bay (mean Wr = 107.1) and Gravine Island (mean Wr = 109.1), where mean Wr was significantly greater (Duncan's Multiple Range Test; $P < 0.05$) during October (all $P < 0.01$). Monthly variation was significant (one-way ANOVA; month effect) in 2004 at D'Olive Bay, Bay Minette Bay, Gravine Island, and McReynold's Lake (all $P < 0.05$). Significantly higher (Duncan's Multiple Range Test; $P < 0.05$) mean Wr occurred during late winter-early spring D'Olive Bay (February; mean Wr = 117.9) and Bay Minette Bay(March; mean Wr = 102.1), during both fall (October, mean Wr = 101.0) and spring (April, mean Wr = 100.7) at Gravine Island, and during fall (November, mean Wr = 99.7) at McReynold's Lake. Despite significant differences (one-way ANOVA; month effect) at Dennis Lake ($F = 1.93$, $P < 0.05$), months did not vary according to a Duncan's Multiple Range Test ($P < 0.05$).

Appendix G. Length-mass regression equations for fish and crustaceans. Equations are in the form WW = *a*L^{b}, where WW = wet weight (g), L = length (mm), and *a* and *b* are fitted constants. Lengths are in the form of carapace width for crabs, carapace length for crayfish, uropod or telson length for shrimp, and total length for fish.

Taxon	N	Size range (mm)	b	a	R^2
CRUSTACEA					
Callinectes sapidus (blue crab)	55	10-153	2.7699	$1.3848 \cdot 10^{-4}$	0.97
Uca longisignalis (mud crab)	10	14-31	2.7467	$8.4101 \cdot 10^{-4}$	0.90
Order Decapoda (crayfish)	20	11-38	2.7722	$7.6208 \cdot 10^{-4}$	0.97
Penaeus setiferus (white shrimp)	11	10-22	3.5282	$2.3286 \cdot 10^{-4}$	0.90
Palaemonetes spp. (grass shrimp)	7	3-5	2.1360	$9.3411 \cdot 10^{-3}$	0.94
FISH					
Alosa chrysochloris (skipjack herring)	14	39-276	2.7150	$3.7265 \cdot 10^{-5}$	0.88
Anchoa mitchelli (bay anchovy)	14	32-65	3.0776	$5.0764 \cdot 10^{-6}$	0.98
Anguilla rostrata (American eel)	18	130-659	3.1015	$1.0957 \cdot 10^{-6}$	0.99
Aplodinotus grunniens (freshwater drum)	5	54-291	3.1983	$3.4610 \cdot 10^{-6}$	0.99
Aphredoderus sayanus (pirate perch)	8	51-67	3.2512	$4.3132 \cdot 10^{-6}$	0.90
Brevoortia patronus (gulf menhaden)	20	37-111	3.2633	$2.8907 \cdot 10^{-6}$	0.998
Cynoscion arenarius (sand seatrout)	22	19-52	2.7430	$2.9468 \cdot 10^{-5}$	0.98
Dormitator maculatus (fat sleeper)	78	55-110	3.0850	$9.0353 \cdot 10^{-6}$	0.92
Dorosoma petenense (threadfin shad)	33	54-123	2.9228	$1.1613 \cdot 10^{-5}$	0.96
Esox niger (chain pickerel)	20	112-228	3.3662	$7.8534 \cdot 10^{-7}$	0.99
Etheostoma fusiforme (swamp darter)	13	31-61	3.1264	$4.6946 \cdot 10^{-6}$	0.96
Fundulus blairae (w. starhead topminnow)	28	20-59	3.3159	$2.2343 \cdot 10^{-6}$	0.97
Fundulus cingulatus (banded topminnow)	8	24-72	2.9842	$1.0510 \cdot 10^{-5}$	0.91
Fundulus chrysotus (golden topminnow)	14	21-75	2.9353	$1.4217 \cdot 10^{-5}$	0.97
Fundulus grandis (gulf killifish)	27	51-102	3.3930	$2.1923 \cdot 10^{-6}$	0.99
Gambusia affinus (mosquitofish)	31	20-45	2.7055	$2.6454 \cdot 10^{-5}$	0.89
Gobionellus oceanicus (highfin goby)	8	42-148	2.8653	$7.7482 \cdot 10^{-6}$	0.99
Ictalurus punctatus (channel catfish)	11	75-191	2.4624	$9.4626 \cdot 10^{-5}$	0.86
Leiostomus xanthurus (spot)	38	42-159	3.0451	$9.4167 \cdot 10^{-6}$	0.995
Lepomis gulosus (warmouth sunfish)	64	38-210	3.1947	$7.3376 \cdot 10^{-6}$	0.99
Lepomis macrochirus (bluegill)	72	22-129	3.1923	$9.4622 \cdot 10^{-6}$	0.98
Lepomis microlophus (redear sunfish)	52	38-138	3.1538	$8.3150 \cdot 10^{-6}$	0.99
Lepomis punctatus miniatus (red-spotted sunfish)	47	39-143	3.1448	$9.7342 \cdot 10^{-6}$	0.99

FISH (cont'd)					
Lucania parva (rainwater killifish)	67	20-97	2.9916	$1.1262 \cdot 10^{-5}$	0.87
Menidia beryllina (inland silverside)	31	33-96	2.7098	$1.9134 \cdot 10^{-5}$	0.92
Microgobius gulosus (clown goby)	18	31-75	2.7074	$2.2683 \cdot 10^{-5}$	0.98
Micropterus salmoides (largemouth bass)	18	82-130	3.0278	$1.0814 \cdot 10^{-5}$	0.99
Myrophis punctatus (speckled worm eel)	8	107-266	2.2651	$2.4166 \cdot 10^{-5}$	0.82
Notemigonus crysoleucas (golden shiner)	14	76-182	3.3790	$1.3191 \cdot 10^{-6}$	0.87
Notropis candidus (silverside shiner)	14	44-86	3.2933	$2.0583 \cdot 10^{-6}$	0.97
Notropis petersoni (coastal shiner)	12	27-70	2.7146	$2.1652 \cdot 10^{-5}$	0.98
Opsopoedus emiliae (pugnose minnow)	5	52-60	1.9991	$4.2423 \cdot 10^{-4}$	0.90
Syngnathus louisianae (chain pipefish)	10	63-115	3.3342	$1.0408 \cdot 10^{-7}$	0.88
Trinectes maculatus (hogchoker)	6	40-68	3.6238	$1.2142 \cdot 10^{-6}$	0.97

Appendix H. Number and percent by number of prey consumed at downstream sites in each season during 2002.

Season	Species	N	%
Winter	*Callinectes sapidus* (blue crab)	11	48
	Lucania parva (rainwater killifish)	1	4
	Syngnathus louisianae (chain pipefish)	2	9
	Penaeus setiferus (white shrimp)	5	22
	Uca longisignalis (fiddler crab)	1	4
	unidentified fish	3	13
Spring	*Anchoa mitchelli* (bay anchovy)	1	2
	Callinectes sapidus (blue crab)	24	53
	Ictalurus punctatus (channel catfish)	1	2
	Micropterus salmoides (largemouth bass)	1	2
	Syngnathus louisianae (chain pipefish)	3	7
	Penaeus setiferus (white shrimp)	2	4
	Uca longisignalis (fiddler crab)	1	2
	unidentified fish	12	27
Summer	*Callinectes sapidus* (blue crab)	76	52
	Cynoscion arenarius (sand seatrout)	1	1
	Leiostomus xanthurus (spot)	1	1
	Lucania parva (rainwater killifish)	3	2
	Menidia beryllina (inland silverside)	1	1
	Penaeus setiferus (white shrimp)	21	14
	Syngnathus louisianae (chain pipefish)	18	12
	Uca longisignalis (fiddler crab)	3	2
	unidentified fish	21	14
Fall	*Anchoa mitchelli* (bay anchovy)	3	3
	Callinectes sapidus (blue crab)	26	27
	Gambusia affinus (mosquitofish)	1	1
	Lepomis macrochirus (bluegill)	1	1
	Menidia beryllina (inland silverside)	1	1
	Microgobius gulosus (clown goby)	1	1
	Notemigonus crysoleucas (golden shiner)	1	1
	Syngnathus louisianae (chain pipefish)	7	7
	Penaeus setiferus (white shrimp)	4	4
	Uca longisignalis (fiddler crab)	1	1
	unidentified fish	49	52

Appendix I. Number and percent by number of prey consumed at upstream sites in each season during 2002.

Season	Species	N	%
Winter	*Anguilla rostrata* (American eel)	1	5
	Callinectes sapidus (blue crab)	4	18
	Menidia beryllina (inland silverside)	1	5
	Microgobius gulosus (clown goby)	1	5
	Penaeus setiferus (white shrimp)	2	9
	Uca longisignalis (fiddler crab)	3	14
	larval shrimp	3	14
	unidentified fish	7	32
Spring	*Callinectes sapidus* (blue crab)	1	4
	Notemigonus crysoleucas (golden shiner)	1	4
	Order Decapoda (crayfish)	1	4
	larval shrimp	24	89
Summer	*Anchoa mitchelli* (bay anchovy)	1	2
	Callinectes sapidus (blue crab)	25	43
	Dorosoma petenense (threadfin shad)	2	3
	Lucania parva (rainwater killifish)	1	2
	Fundulus blairae (western starhead topminnow)	1	2
	Menidia beryllina (inland silverside)	3	5
	Lepomis punctatus miniatus (red-spotted sunfish)	2	3
	Penaeus setiferus (white shrimp)	4	7
	Uca longisignalis (fiddler crab)	6	10
	unidentified fish	13	22
Fall	*Callinectes sapidus* (blue crab)	5	7
	Dormitator maculatus (fat sleeper)	37	50
	Lepomis microlophus (redear sunfish)	4	5
	Lepomis punctatus miniatus (red-spotted sunfish)	1	1
	Lucania parva (rainwater killifish)	1	1
	Mysid shrimp	1	1
	Penaeus setiferus (white shrimp)	4	5
	Syngnathus louisianae (chain pipefish)	1	1
	Uca longisignalis (fiddler crab)	1	1
	unidentified fish	19	26

Appendix J. Number and percent by number of prey consumed at downstream sites in each season during 2003.

Season	Species	N	%
Winter	*Callinectes sapidus* (blue crab)	8	50
	Esox niger (chain pickerel)	1	6
	Palaemonetes spp. (grass shrimp)	3	19
	Syngnathus louisianae (chain pipefish)	1	6
	Uca longisignalis (fiddler crab)	1	6
	unidentified fish	2	13
Spring	*Anchoa mitchelli* (bay anchovy)	7	3
	Brevoortia patronus (gulf menhaden)	2	1
	Callinectes sapidus (blue crab)	11	4
	Larval shrimp	53	21
	Lepomis macrochirus (bluegill)	1	<0.5
	Lepomis microlophus (redear sunfish)	1	<0.5
	Lucania parva (rainwater killifish)	3	1
	Mysid shrimp	63	25
	Order Amphipoda (amphipod)	25	10
	Order Decapoda (crayfish)	1	<0.5
	Palaemonetes spp. (grass shrimp)	36	15
	Penaeus setiferus (white shrimp)	10	4
	Syngnathus louisianae (chain pipefish)	1	<0.5
	Uca longisignalis (fiddler crab)	9	4
	unidentified fish	25	10
Summer	*Callinectes sapidus* (blue crab)	25	38
	Lucania parva (rainwater killifish)	1	2
	Micropterus salmoides (largemouth bass)	2	3
	Order Amphipoda (amphipod)	1	2
	Order Decapoda (crayfish)	1	2
	Palaemonetes spp. (grass shrimp)	3	5
	Syngnathus louisianae (chain pipefish)	3	5
	Uca longisignalis (fiddler crab)	8	12
	unidentified fish	21	32
Fall	*Anchoa mitchelli* (bay anchovy)	1	<0.5
	Brevoortia patronus (gulf menhaden)	1	<0.5
	Callinectes sapidus (blue crab)	36	17
	Fundulus blairae (western starhead topminnow)	2	1
	Lepomis gulosus (warmouth sunfish)	2	1
	Lepomis macrochirus (bluegill)	4	2
	Lepomis microlophus (redear sunfish)	2	1
	Lepomis punctatus miniatus (red-spotted sunfish)	15	7
	Lucania parva (rainwater killifish)	34	16
	Menidia beryllina (inland silverside)	1	<0.5

Fall (cont'd.)	*Myrophis punctatus* (speckled worm eel)	1	<0.5
	Mysid shrimp	76	35
	Notropis candidus (silverside shiner)	2	1
	Order Amphipoda (amphipod)	1	<0.5
	Palaemonetes spp. (grass shrimp)	19	9
	Syngnathus louisianae (chain pipefish)	2	1
	Trinectes maculatus (hogchoker)	1	<0.5
	Uca longisignalis (fiddler crab)	5	2
	unidentified fish	11	5

Appendix K. Number and percent by number of prey consumed at upstream sites in each season 2003.

Season	Species	N	%
Winter	*Callinectes sapidus* (blue crab)	1	4
	Gobionellus oceanicus (highfin goby)	1	4
	Lepomis macrochirus (bluegill)	2	7
	Notropis candidus (silverside shiner)	2	7
	Order Amphipoda (amphipod)	1	4
	Uca longisignalis (fiddler crab)	11	41
	unidentified fish	9	33
Spring	*Anguilla rostrata* (American eel)	1	<0.5
	Callinectes sapidus (blue crab)	2	1
	Esox niger (chain pickerel)	1	<0.5
	Lepomis gulosus (warmouth sunfish)	1	<0.5
	Lepomis macrochirus (bluegill)	2	1
	Microgobius gulosus (clown goby)	1	<0.5
	Micropterus salmoides (largemouth bass)	1	<0.5
	Mysid shrimp	162	61
	Order Amphipoda (amphipod)	6	2
	Order Decapoda (crayfish)	4	2
	Palaemonetes spp. (grass shrimp)	59	22
	Penaeus setiferus (white shrimp)	4	2
	Syngnathus louisianae (chain pipefish)	3	1
	Uca longisignalis (fiddler crab)	1	<0.5
	unidentified fish	17	6
Summer	*Anchoa mitchelli* (bay anchovy)	1	2
	Callinectes sapidus (blue crab)	1	2
	Ictalurus punctatus (channel catfish)	1	2
	Lepomis gulosus (warmouth sunfish)	1	2
	Lepomis macrochirus (bluegill)	1	2
	Lepomis microlophus (redear sunfish)	1	2
	Lepomis punctatus miniatus (red-spotted sunfish)	1	2
	Lucania parva (rainwater killifish)	1	2
	Micropterus salmoides (largemouth bass)	1	2
	Mysid shrimp	1	2
	Order Amphipoda (amphipod)	1	2
	Order Decapoda (crayfish)	2	5
	Palaemonetes spp. (grass shrimp)	10	24
	Uca longisignalis (fiddler crab)	1	2
	unidentified fish	18	43
Fall	*Brevoortia patronus* (gulf menhaden)	4	5
	Callinectes sapidus (blue crab)	6	7
	Lepomis macrochirus (bluegill)	2	2

Fall (cont'd.)	*Lepomis punctatus miniatus* (red-spotted sunfish)	2	2
	Notropis candidus (silverside shiner)	3	4
	Mysid shrimp	38	47
	Order Amphipoda (amphipod)	1	1
	Order Decapoda (crayfish)	1	1
	Palaemonetes spp. (grass shrimp)	3	4
	unidentified fish	21	26

Appendix L. Number and percent by number of prey consumed at downstream sites in each season during 2004.

Season	Species	N	%
Winter	*Callinectes sapidus* (blue crab)	38	16
	Family Carangidae (unidentified jack)	23	10
	Lepomis gulosus (warmouth sunfish)	1	<0.5
	Lepomis macrochirus (bluegill)	5	2
	Lepomis microlophus (redear sunfish)	1	<0.5
	Lepomis punctatus miniatus (red-spotted sunfish)	4	2
	Lucania parva (rainwater killifish)	1	<0.5
	Microgobius gulosus (clown goby)	3	1
	Notropis petersoni (coastal shiner)	1	<0.5
	Order Amphipoda (amphipod)	11	5
	Order Decapoda (crayfish)	6	3
	Palaemonetes spp. (grass shrimp)	120	52
	Syngnathus louisianae (chain pipefish)	1	<0.5
	Uca longisignalis (fiddler crab)	1	<0.5
	unidentified fish	15	6
Spring	*Aplodinotus grunniens* (freshwater drum)	1	<0.3
	Brevoortia patronus (gulf menhaden)	11	3
	Callinectes sapidus (blue crab)	63	17
	Cyprinodon variegatus (sheepshead minnow)	1	<0.3
	Enneacanthus gloriosus (blue-spotted sunfish)	2	1
	Esox niger (chain pickerel)	1	<0.3
	Fundulus grandis (gulf killifish)	1	<0.3
	Gobionellus oceanicus (highfin goby)	1	<0.3
	Lepomis gulosus (warmouth sunfish)	1	<0.3
	Lepomis macrochirus (bluegill)	1	<0.3
	Lepomis microlophus (redear sunfish)	1	<0.3
	Lucania parva (rainwater killifish)	4	1
	Menidia beryllina (inland silverside)	8	2
	Microgobius gulosus (clown goby)	4	1
	Micropterus salmoides (largemouth bass)	2	1
	Mysid shrimp	117	31
	Notemigonus crysoleucas (golden shiner)	1	<0.3
	Notropis petersoni (coastal shiner)	1	<0.3
	Order Amphipoda (amphipod)	11	3
	Order Decapoda (crayfish)	24	6
	Palaemonetes spp. (grass shrimp)	90	24
	Penaeus setiferus (white shrimp)	3	1
	Uca longisignalis (fiddler crab)	4	1
	unidentified fish	19	5
Summer	*Callinectes sapidus* (blue crab)	15	2

Summer (cont'd.)	*Fundulus cingulatus* (banded topminnow)	1	<0.2
	Leiostomus xanthurus (spot)	4	1
	Lepomis punctatus miniatus (red-spotted sunfish)	1	<0.2
	Lucania parva (rainwater killifish)	2	<0.4
	Mysid shrimp	575	88
	Order Decapoda (crayfish)	6	1
	Palaemonetes spp. (grass shrimp)	25	4
	Syngnathus louisianae (chain pipefish)	2	<0.4
	Uca longisignalis (fiddler crab)	11	2
	unidentified fish	11	2
Fall	*Callinectes sapidus* (blue crab)	134	71
	Lepomis macrochirus (bluegill)	2	1
	Lepomis microlophus (redear sunfish)	1	1
	Microgobius gulosus (clown goby)	1	1
	Mysid shrimp	10	5
	Order Amphipoda (amphipod)	3	2
	Order Decapoda (crayfish)	2	1
	Palaemonetes spp. (grass shrimp)	8	4
	Penaeus setiferus (white shrimp)	1	1
	Syngnathus louisianae (chain pipefish)	1	1
	Uca longisignalis (fiddler crab)	4	2
	unidentified fish	22	12

Appendix M. Number and percent by number of prey consumed at upstream sites in each season during 2004.

Season	Species	N	%
Winter	*Callinectes sapidus* (blue crab)	6	10
	Enneacanthus gloriosus (blue-spotted sunfish)	1	2
	Fundulus grandis (gulf killifish)	1	2
	Lepomis macrochirus (bluegill)	6	10
	Lepomis punctatus miniatus (red-spotted sunfish)	6	10
	Microgobius gulosus (clown goby)	1	2
	Micropterus salmoides (largemouth bass)	3	5
	Notropis candidus (silverside shiner)	1	2
	Order Decapoda (crayfish)	1	2
	Palaemonetes spp. (grass shrimp)	10	17
	Uca longisignalis (fiddler crab)	4	7
	unidentified fish	18	31
Spring	*Alosa chrysochloris* (skipjack herring)	1	<0.2
	Anchoa mitchelli (bay anchovy)	1	<0.2
	Aphredoderus sayanus (pirate perch)	2	<0.4
	Brevoortia patronus (gulf menhaden)	4	1
	Callinectes sapidus (blue crab)	10	2
	Enneacanthus gloriosus (blue-spotted sunfish)	1	<0.2
	Esox niger (chain pickerel)	1	<0.2
	Etheostoma fusiforme (swamp darter)	1	<0.2
	Fundulus chrysotus (golden topminnow)	1	<0.2
	Lepomis macrochirus (bluegill)	2	<0.4
	Lepomis microlophus (redear sunfish)	4	1
	Lepomis punctatus miniatus (red-spotted sunfish)	7	1
	Lucania parva (rainwater killifish)	7	1
	Micropterus salmoides (largemouth bass)	1	<0.2
	Mysid shrimp	420	80
	Notropis texanus (weed shiner)	1	<0.2
	Order Amphipoda (amphipod)	12	2
	Order Decapoda (crayfish)	15	3
	Palaemonetes spp. (grass shrimp)	9	2
	Penaeus setiferus (white shrimp)	1	<0.2
	Uca longisignalis (fiddler crab)	2	<0.4
	unidentified fish	25	5
Summer	*Brevoortia patronus* (gulf menhaden)	2	<0.2
	Callinectes sapidus (blue crab)	6	1
	Fundulus blairae (western starhead topminnow)	2	<0.2
	Lucania parva (rainwater killifish)	1	<0.01
	Microgobius gulosus (clown goby)	3	<0.3
	Micropterus salmoides (largemouth bass)	4	<0.4

Summer (cont'd.)	Mysid shrimp	961	96
	Order Decapoda (crayfish)	3	<0.3
	Palaemonetes spp. (grass shrimp)	5	<0.5
	Penaeus setiferus (white shrimp)	1	<0.01
	Uca longisignalis (fiddler crab)	4	<0.4
	unidentified fish	10	1
Fall	*Anchoa mitchelli* (bay anchovy)	1	<0.2
	Callinectes sapidus (blue crab)	33	6
	Dorosoma petenense (threadfin shad)	1	<0.2
	Lepomis macrochirus (bluegill)	1	<0.2
	Micropterus salmoides (largemouth bass)	1	<0.2
	Mysid shrimp	487	89
	Notropis candidus (silverside shiner)	1	<0.2
	Opsopoedus emiliae (pugnose minnow)	1	<0.2
	Order Decapoda (crayfish)	2	<0.4
	Uca longisignalis (fiddler crab)	1	<0.2
	unidentified fish	18	3